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Integrating climate change into conservation and restoration strategies: the case of the Tasmanian eucalypts

by

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(Hons)

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Statement of co-authorship

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The candidate led and was responsible for all aspects of the work undertaken in the thesis, including the development of ideas, field and laboratory work, data analysis, and writing of manuscripts/chapters. The supervisory team was led by BMP and REV, and provided the candidate with overall guidance during the development of ideas, data analysis, and writing. RMBH provided guidance during the development of Chapter 4 and contributed to revisions before publication of Chapter 4, as well as providing access to the climate layers derived as part of the Climate Futures of Tasmania. TGB assisted in the sample collections and the establishment and monitoring of the common garden field trials, as well as contributed to revisions of Chapters 5 and 6.

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Abstract

Global climate change will negatively impact major components of the world's biodiversity over the next century, and there is an increasing need for strategies and tools to guide species conservation and management. This issue is particularly relevant to species and provenance choices in ecological restoration where diverse strategies have been proposed to ensure future climate resilience. This thesis focuses on the *Eucalyptus* tree flora of the island of Tasmania, Australia, assessing the likely change in species modelled suitable habitat, and strategies for identifying suitable species and provenances for restoration tree plantings. This is a topical issue as the long-standing 'local-is-best' paradigm in ecological restoration is being increasingly questioned in the face of global climate change.

Habitat suitability models were used to determine whether a eucalypt species susceptibility to future climate change (based on 2020, 2050 and 2080 projections) can be predicted by evolutionary history, habitat type or distribution pattern. A large extent of the modelled current climate habitat will be lost by the end of this century and 63% of records will be outside of modelled suitable habitat. Species from subalpine habitats were most at risk of maladaptation under future climate change. Susceptibility was not linked to evolutionary history or distribution pattern. Despite the loss of suitable climate habitat, many of the current conservation reserves still maintained populations of species that will not be at risk of climate maladaptation by 2080.

To assist in guiding species choice for our target restoration region (the Midlands), we used the same climate projections to model the suitability of regionally local and non-local species through space and time. We identified one non-local and ten regionally local candidate species that would not be maladapted to the future climate habitat of the Midlands. The predicted decrease in the suitability of most local species in the future was compensated by the northern expansion of predicted suitable habitat for a regionally local and non-local species well outside their current distribution range.

A framework was subsequently developed to identify provenances of targeted restoration species likely to be best adapted to the future climates of restoration sites to test and implement climate-adjusted provenancing. This framework accounted for inbreeding risk through habitat fragmentation and was translated into software (Provenancing Using Climate Analogues [PUCA]). This software matched current and future climate predictions for restoration sites to known provenances of the target species that are already growing in analogous climates for 2020, 2050 and 2080 projections. I demonstrate the application of PUCA and identified key outstanding assumptions which need empirical validation.

Experimental trials were established to test the assumptions of the PUCA model and identify the climate components which have shaped adaptive variation among the provenances of a key restoration species *E. ovata*. A germination trial showed that provenance home-site climate effects did not affect seed germination characteristics. A glasshouse and a common garden field trial were established using range-wide collections of open-pollinated seed from 45 provenances (collected from 312 individuals), to study how home-site climate affects seedling functional traits and early field performance. Two orthogonal climate vectors (representing aridity and frost gradients) were shown to shape adaptive variation among provenances in seedling functional traits. Predicted changes in these vectors from contemporary to 2080 were spatially mapped as an alternative approach to predict (i) the adaptive limits of the species, (ii) the change in the climate selective surface, and (iii) provenance transfer functions. Only two-year performance data was available for the field trial, and this revealed little evidence of maladaptation of provenances from homes-sites spanning the selective gradient. The demonstration that provenances from future analogous environments have a broad transfer function and can be successfully established in restoration plantings is important for long-lived trees, as future-adapted individuals must establish under current climate regimes.

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Other Published Work

While undertaking the current study, I have also authored and co-authored a number of works that were not included in this thesis. Below I list the refereed and unrefereed publications that were produced during the course of this thesis.

Refereed publications

1. Mokany K, Jordan GJ, Harwood TD, **Harrison PA**, Keppel G, Gilfedder L, Carter O, Ferrier S (2017) Past, present and future refugia for Tasmania's palaeoendemic flora. *Journal of Biogeography*. DOI:10.1111/jbi.12927.

2. Prober, SM, Potts, BM, Bailey, T, Byrne, M, Dillon, S, **Harrison, PA**, Hoffmann, AA, Jordan, R, McLean, EH, Steane, DA, Stock, WD & Vallincourt, RE (2016) Climate adaptation and ecological restoration in eucalypts. *Proceedings of the Royal Society of Victoria*, **128**, 40-53.

3. Jordan GJ, **Harrison PA**, Worth JRP, Williamson GJ, Kirkpatrick JB (2016) Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. *Global Ecology and Biogeography* **25**, 127-140.

4. Worth JRP, **Harrison PA**, Williamson GJ, Jordan GJ (2014) Whole range and regional-based ecological niche models predict differing exposure to 21st century climate change in the key cool temperate rainforest tree southern beech (*Nothofagus cunninghamii*). *Austral Ecology* **40**, 126-138.

5. **Harrison PA**, Jones RC, Vaillancourt RE, Wiltshire RJE, Potts BM (2014) Unravelling the evolutionary history of *Eucalyptus cordata* (Myrtaceae) using molecular markers. *Australian Journal of Botany* **62**, 114-131.

Unrefereed publications

1. **Harrison PA**, Vaillancourt RE, Bailey TG, Davidson N, Potts BM (2017) Modelling the climate change impacts on the Tasmanian eucalypt flora. 'Climate change and conservation properties', Campbell Town, Australia. 11 May 2017 (Invited talk)

2. **Harrison PA** (2017) AUSClim: an R package to acquire daily climate observations and calculate climate variables.

3. Weller-Wong A, Bailey TG, Gauli A, **Harrison PA**, Vaillancourt RE, Potts BM (2017) Predicting provenance performance in restoration plantings of *Eucalyptus pauciflora* in the Tasmanian Midlands. (Poster)

4. Bailey TG, **Harrison PA**, Gauli A, Whitmore J, Vaillancourt RE, Davidson N, Potts BM (2017) Is local best? Testing forest tree provenancing strategies using field trials embedded in restoration plantings in Tasmania. (Talk)

5. **Harrison PA** (2016) PUCA: an R package to predict provenances using climate analogues.

6. Bailey TG, **Harrison PA**, Gauli A, Whitmore J, Vaillancourt RE, Davidson N, Potts BM (2016) Establishing resilient ecological restoration in the face of future climate change uncertainty. 'Australian Forest Growers 2016 Biennial National Conference'. Launceston, Australia. 23-26 October 2016. (Invited talk)

7. Steane DA**, Harrison PA**, Prober SM, Byrne M, McLean E, Stock WD, Bailey TG, Vaillancourt RE, Potts BM (2016) Using genomic information to increase resilience of forest tree plantings. 'IUFRO Genomics and Tree Genetics, IUFRO Subdivision 2.4 (Genetics)'. Arcachon, France. 30 May – 3 June 2016. (Talk).

8. Prober SM, Bailey TG, Byrne M, Dillon S, **Harrison PA**, Hoffmann AA, Jordan R, McLean E, Potts BM, Steane DA, Stock WD, Vaillancourt RE (2016) Adaption to climate in widespread eucalypts. Symposium on 'Conserving Eucalypts – the Why and the How'. The Royal Society of Victoria, Melbourne, Victoria. 18 March 2016. (Invited presentation; http://www.royalsocietyvictoria.org.au/wp-content/uploads/EucSymBooklet_V3-1.pdf).

9. Steane DA**, Harrison PA**, Prober SM, Byrne M, McLean E, Stock WD, Bailey TG, Vaillancourt RE, Potts BM (2016) Climate-adjusted provenancing: constructing forests for the future. 'Species on The Move'. Hobart, Tasmania. 10-12 February 2016. (Talk; http://www.speciesonthemove.com/provisional-program).

10. Potts BM, **Harrison PA** (2015) Climate change and tree genetics. 'Ecological Society of Australia Landscape forum: Knowledge exchange on climate change', University of Tasmania, Hobart, Australia. 30 March 2015. (Invited presentation).

11. Potts BM, **Harrison PA**, Bailey TG, Steane DA, Vaillancourt RE, Tilyard P, Davidson NJ (2015) Climate adaptation and provenance choice for revegetation: Insights from *Eucalyptus*. 'Seeds for success: a forum on revegetation and climate change', La Trobe University, Australia. 9 July 2015. (Invited presentation; http://murrumbidgeelandcare.asn.au/files/Seeds%20for%20Success%20Forum%20Agenda.pdf).

12. Davidson NJ, Bailey TG, Gauli A, **Harrison PA**, Steane DA, Vaillancourt RE, Potts BM (2014) Providing a genetic framework to enhance the success and benefits from forest restoration and carbon plantings in the rural Midlands of Tasmania, Australia. '2nd Conference of Society for Ecological Restoration Australasia'. Noumea, New Caledonia. 17-21 November 2014. (Talk; http://www.seraustralasia.com/conference2014/speakers.pdf).

13. **Harrison PA**, Bailey TG, Vaillancourt RE, Potts BM (2014). The effects of fragmentation, geography and climate on forest tree reproduction. '10th Australasian Plant Conservation Conference'. Hobart, Australia. 12-13 November 2014. (Talk; http://www.anbg.gov.au/anpc/conferences/2014/WEB%203.1_13112014.pdf).

14. Steane DA, Potts BM, McLean E, Prober SM, Stock WD, Vaillancourt RE, **Harrison PA**, Byrne M (2014). Detecting signals of local adaptation in widespread species. 'Phylomania 2014'. University of Tasmania, Hobart, Australia. 5-7 November 2014. (Talk).

15. **Harrison PA** (2013) Establishing a framework to enhance the conservation of the critically endangered endemic, *Eucalyptus gunnii* subsp. *divaricata*. Tasmanian Land Conservancy, Hobart.

Table of Contents

List of Tables

List of Figures

Chapter 1: General introduction

This thesis is a study on the integration of current and future climate change into the conservation and ecological restoration of forest ecosystems, with a particular focus on the diverse eucalypt flora of Tasmania, Australia. This general introduction provides an overview of the current and future trends in global climates, with a focus on continental-level climate change across Australia and regional-level variation within Tasmania. It then briefly reviews the impact of climate change on managing natural resources, highlighting the effect that current climate change is having on global forest ecosystems, the challenges faced by conservation ecologists in the face of climate change, and the tools available to guide conservation decisions. It then discusses the field of ecological restoration as a key provider of strategies to conserve biodiversity and ecosystem services. In doing so, it provides an overview of the traditional 'local-is-best' approach to ecological restoration while highlighting the potential caveats of this approach in an era of global change (land-use change and climate change), as well as briefly introducing alternative strategies that have been proposed to bolster genetic diversity and promote the long term climate-resilience of the ecological plantings under future environmental flux. It then concludes by providing an overview of the plight faced by the Australian eucalypt woodlands, with a particular focus on the eucalypt woodlands of the Tasmanian Midlands, which is the focus restoration region of this thesis, and gives a brief introduction to the focal study species *Eucalyptus ovata*. An outline of the chapters presented in this thesis is provided.

1.1 A global perspective on current and future trends in climate change

1.1.1 Observed and projected changes in temperature

There is little doubt that global temperatures have rapidly changed over the last century. The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) reported that the

global mean annual temperature has increased by +0.85 ˚C since 1880 (IPCC 2014), with global temperatures increasing by over a +0.1 ˚C since the Fourth Assessment Report of the IPCC in 2007. Observed changes in global mean annual temperature have been spatially heterogeneous (Figure 1.1a), with higher latitudes in the Northern Hemisphere and in South America showing nearly a two-fold increase in mean annual temperatures (+1.75 ˚C; IPCC 2014). Australia is close to the world average, with mean annual temperatures warming on average by +0.9 ˚C since 1910 (CSIRO and Bureau of Meteorology 2015). Indeed, temperatures have been increasing on average by +0.15 ˚C per decade across Australia, with the interior showing the greatest rate of change (Figure 1.1c). The decadal rate of temperature change is comparable to that of many of the biogeographic regions (hereafter bioregions) within the island of Tasmania. The northern bioregions of Tasmania show the greatest mean change (grand mean: +0.8 ˚C; Furneaux: +0.7 ˚C; King: +0.9 ˚C; Northern Slopes: +0.8 ˚C) since the detectable signal of pre-industrial warming in the Southern Hemisphere (baseline pre-industrial period: 1911-1959; Abrams *et al*. 2016) (Figure 1.2).

The IPCC predicts a considerable intensification of global mean annual temperatures into the near and distant future, with projected temperatures during the 2016 – 2035 period to be in the range of +0.3 ˚C to +0.7 ˚C warmer (relative to 1986 – 2005) and up to +2.6 ˚C to +4.8 ˚C warmer by the end of this century (IPCC 2014). Intensifications in mean annual temperature are projected to be most extreme in higher latitudes of the Northern Hemisphere where temperatures are expected to be anywhere between +3 ˚C to +11 ˚C warmer than present (IPCC 2014). By the end of this century, mean annual temperatures in Australia are projected to be between +2.8 ˚C to +5.1 ˚C warmer than the contemporary (1986 – 2005) mean, with a clear poleward redistribution of temperature extremes (CSIRO and Bureau of Meteorology 2015). Indeed, the mean annual temperatures in Southern and Eastern Australia are projected to increase on average by +3.5 ˚C (CSIRO and Bureau of

Meteorology 2015), with a relatively uniform intensification of mean annual temperatures in Tasmania (Figure 1.2).

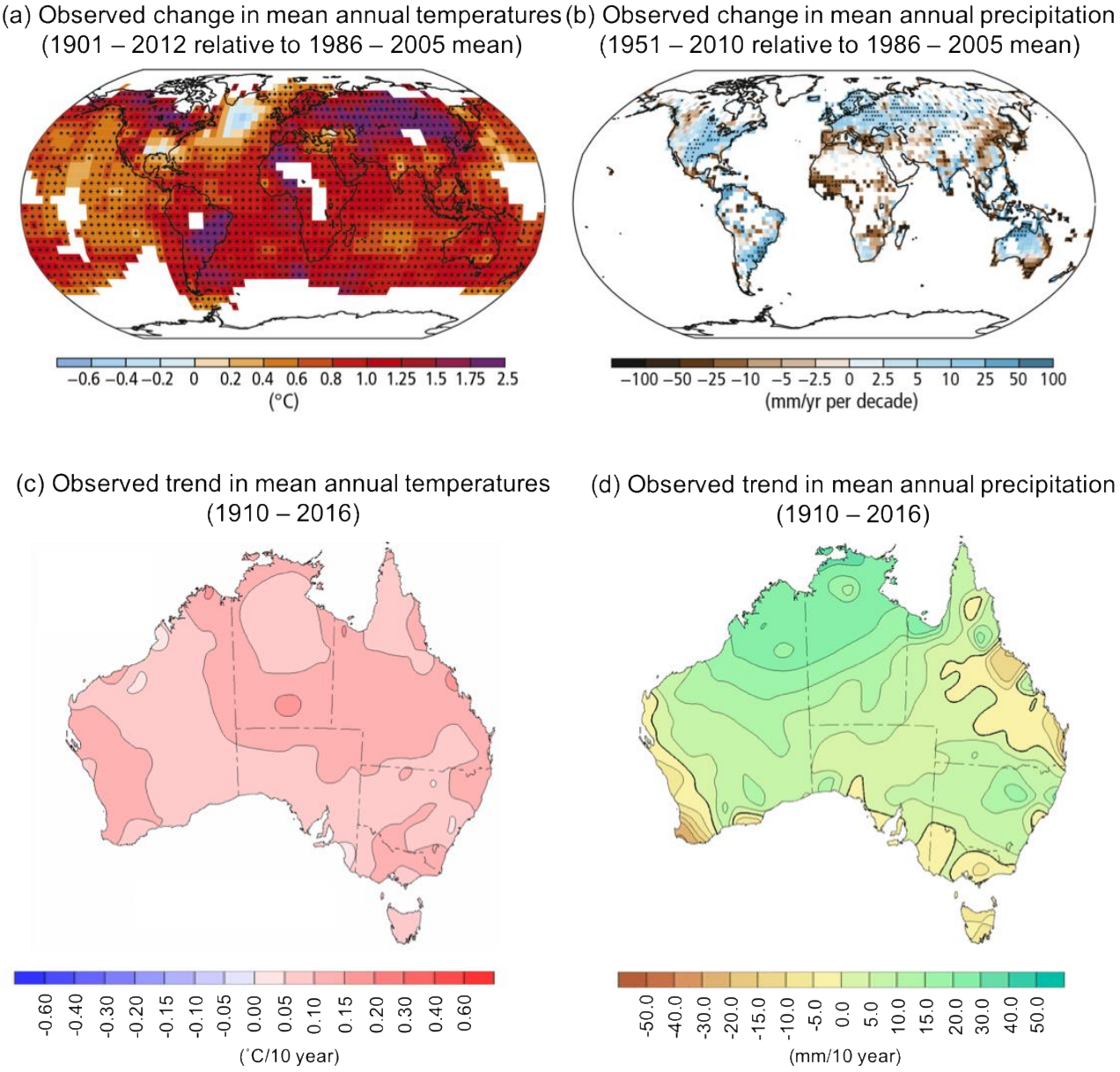
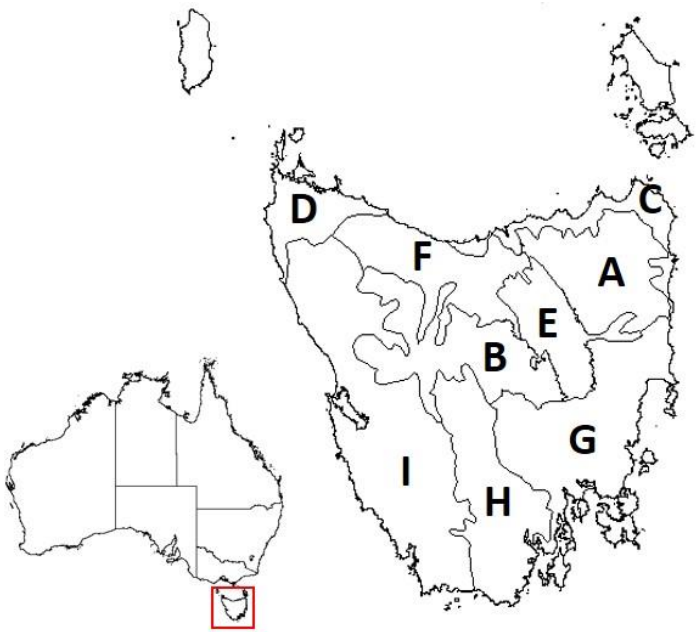
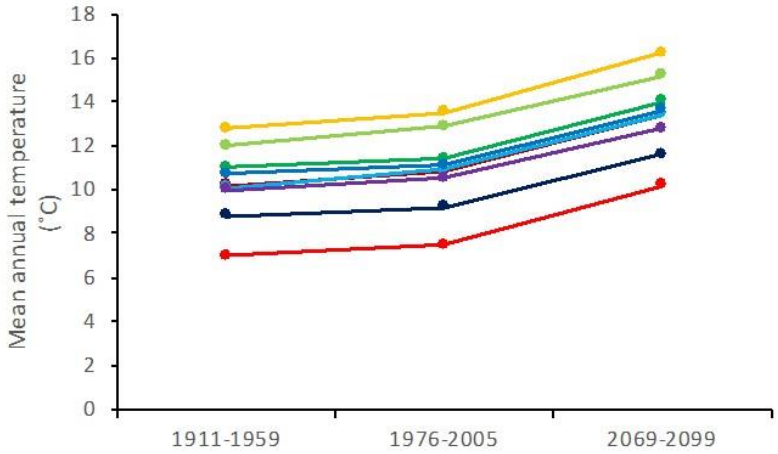


Figure 1.1. Map of global change in the mean annual temperature (a) and precipitation (b) over the 1901-2012 period relative to the mean of the 1986-2005 period, derived from a linear regression. Also shown is the observed decadal trend in mean annual temperature (c) and precipitation (d) for the Australian continent. Australian climate data obtained from the Bureau of Meteorology (http://www.bom.gov.au/climate/change; accessed 30 May 2017). Global maps of observed change in temperature and precipitation were reproduced from Figure 1.1 in IPCC (2014).



Region	Decadal rate of change (1911-2016)	
	Mean annual temperature (˚C/decade)	Mean annual precipitation (mm/decade)
A Ben Lomond	0.10	- 4
B Central Highlands	0.10	- 8
C Furneaux	0.11	- 3
D King	0.12	-7
E Northern Midlands	0.10	-2
F Northern Slopes	0.11	-4
G South East	0.10	-5
H Southern Ranges	0.10	-15
I West	0.10	-37



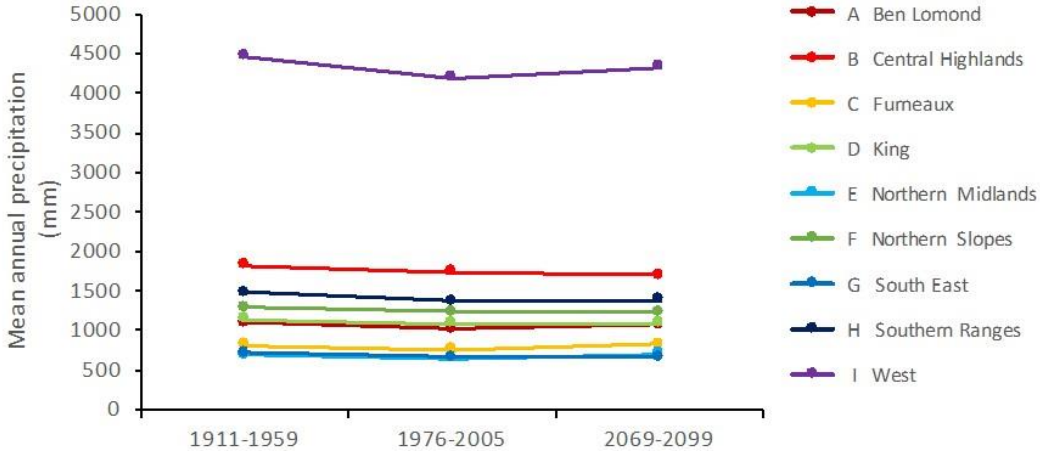


Figure 1.2 (on page 4). Change in regional-level climate across the island of Tasmania. Top-right panel shows the southern location of Tasmania relative to the Australian continent and the nine Interim Biogeographic Regionalisation for Australia (IBRA) regions within Tasmania. Top-left panel shows the decadal rate of change in mean annual temperature and precipitation. Bottom panels show the mean change for each bioregion in Tasmania for mean annual temperature (left side) and mean annual precipitation (right side) during the period prior to the detection of climate change in the Southern Hemisphere (pre-1959; Abrams *et al.* 2016), the contemporary baseline climate (1976-2005; Xu and Hutchinson 2012), and the projected climate by the end of this century (2069-2099). Daily minimum and maximum temperature and precipitation surfaces from 1911-2016 for Tasmania were derived by Jones *et al.* (2009) and were obtained from the Australian Bureau of Meteorology. Projected climate was calculated as the sum of the contemporary baseline climate and the mean change between the contemporary climate and future climate projected by six Global Circulation Models (GCMs) for Tasmania (see Chapter 2 for details on GCMs).

1.1.2 Observed and projected changes in precipitation

Global patterns of precipitation over the past century have been neither spatially nor temporally uniform (Figure 1.1b), with only weak evidence of an overall increase in global precipitation (Dore 2005; IPCC 2014). Rather, it appears that the seasonal pattern, duration, and magnitude of rainfall events over the last century have changed (Easterling *et al.* 2000), and since the early 1950s, global patterns of precipitation have become increasingly varied across space (IPCC 2014). Indeed, consistent with global reports (Kunkel *et al.* 1999; Easterling *et al.* 2000; Wang and Zhou 2005), the frequency of extreme rainfall events have increased in Australia (Dore 2005; CSIRO and Bureau of Meteorology 2015), with an obvious clear decline in precipitation across south-eastern Australia (Figure 1.1d; Nicholls 2006; CSIRO and Bureau of Meteorology 2015). This decline in precipitation is also evident across e most of the Tasmanian bioregions, with the Southern Ranges and West bioregions showing the greatest decline in mean annual precipitation since the detectable signature of climate change in the Southern Hemisphere (Figure 1.2).

There is a relatively high degree of uncertainty in the projected changes of global precipitation, which is most likely due to the often strong dependency of precipitation patterns on other global forcings, such as the North Atlantic Oscillation and the El Nino-Southern Oscillation (Dore 2005; Power *et al.* 2013). Nevertheless, as climates warm, it is likely that the projected changes in

precipitation will not be spatially uniform, with equatorial and higher latitudes projected to experience upwards of +40% increase in precipitation compared to the decreases in precipitation projected for mid-latitude zones (IPCC 2014). This decrease, however, is expected to coincide with an increase in extreme precipitation events (IPCC 2014). The projected decline in precipitation is most evident in Southern and Eastern Australia, were a continued drying trend is projected, along with a southward encroachment of the summer-dominated rainfall zone (CSIRO and Bureau of Meteorology 2015). Regional changes in precipitation are projected to be variable, which is no better demonstrated than in Tasmania (Figure 1.2). While the average projected change in precipitation across the nine bioregions in Tasmania is expected to be relatively minor with most bioregions showing an increase in precipitation (Figure 1.2), the variability within bioregions may be large. For example, the Central Highlands bioregion is projected to experience on average a -45 mm decline in precipitation by the end of this century, however, within this bioregion variability is projected to be large, with precipitation ranging between -214 mm to +326 mm (data not shown).

1.2 Climate change and the management of natural resources

1.2.1 Impacts of current climate change on species

While it is paradoxical to consider the positive impacts of climate change on species, there is evidence that some species have indeed benefited from a warming climate. First, increasing temperatures have permitted plants to increase in abundance. For example, warming in both the Arctic and Antarctic polar regions has facilitated the increased abundance of plant species (Smith 1994; Sturm *et al.* 2001). For example, increasing summer temperatures across Antarctica have been attributed to the enhanced seed maturation, germination, and survival of seedlings which in turn has increased the abundance of *Colobanthus quitensis* and *Deschampsia antarctica* (Smith 1994). Second, the advancement of treelines coinciding with recent climate change has also resulted in an increased richness of species in mountainous regions (Klanderud and Birks 2003). Third, increased

temperatures have coincided with increased net primary productivity of forest ecosystems (Nemani *et al.* 2003). The lengthening of the growing season and advancement of phenological events in response to a warming climate has been attributed to increased productivity in the Northern Hemisphere forest ecosystems (Myneni *et al.* 1997; Cleland *et al.* 2012).

While current and future climate change will likely benefit some species, it is also very likely to negatively impact many species. First, in some areas, the frequency of intense fires has increased coincidently with recent warming (Luo *et al.* 2013; Sharples *et al.* 2016). While fire is a critical component of many species regeneration cycle (Greene *et al.* 1999; Bradbury *et al.* 2016), the increased frequency may have far reaching impacts on fire sensitive components of the flora (Worth *et al.* 2016). Consecutive fires over short time frames may lead to a depletion of the soil or aerial seedbank (Fairman *et al.* 2016), which together with spatial and temporal shifts in the regeneration niche (Mok *et al.* 2011; Sanger *et al.* 2011) may lead to a breakdown in recruitment. Second, temperature-driven expansions of species boundaries has resulted in the competitive exclusion and extirpation of local populations. For example, the warming arctic ecosystems has seen increased invasion of plant species which competitively outcompete lichen for light resources, which has resulted in a contraction of tundra vegetation (Cornelissen *et al.* 2001; Joly *et al.* 2009). Furthermore, recent increases in temperature and precipitation together with high population turnover has been attributed to the upslope expansion of 'northern hardwood' species at the expense of boreal species (Beckage *et al.* 2008). Third, recent warming has seen the expansion of pests and pathogens into previously uninhabitable climates (Bale *et al.* 2002; Bebber *et al.* 2013), where forest species have not been historically pre-disposed to these enemies (Burke *et al.* 2017). For example, drought stress coupled with the lack of low temperature-induced mortality of overwintering mountain pine beetles (*Dendroctonus ponderosae*) led to large outbreaks that caused widespread dieback of *Pinus* species across America (Creeden *et al.* 2014; Buotte *et al.* 2016). Fourth, increased heat- and drought-stress

has been attributed to the widespread die-off across forest ecosystems (Allen *et al.* 2010). For example, extreme heat and water stress were attributed to the severe canopy dieback and stem mortality in *Eucalyptus marginata* forests of Western Australia (Matusick *et al.* 2013).

1.2.2 Challenges in conserving species under current and future climate change

The global fingerprint of climate change is evident across marine (Poloczanska *et al.* 2016), freshwater (Comte *et al.* 2013), and terrestrial ecosystems (Allen *et al.* 2010; Descamps *et al.* 2016). Current and future climate change is adding a further complexity to the management and conservation of natural resources. Not only have species begun to expand and/or contract their range margins (Thomas 2010; Chen *et al.* 2011; Feeley *et al.* 2013; Fisichelli *et al.* 2014; Serra-Diaz *et al.* 2016), but the directional shift of a species range may be in a counter-direction to the widely anticipated poleward or upslope migration (Parmesan *et al.* 2003) and rather towards areas with increased moisture availability (Fei *et al.* 2017). The current and predicted redistribution of species highlights two broad challenges for conservation managers, which are discussed below.

First, there is a need to determine the effectiveness of the current reserve estates that aim to protect species and ecosystems of high conservation value. While reserves are one of the most effective strategies to conserve biodiversity (Shafer 1999), range shifts may result in species either moving outside protected areas or being within maladaptive environments in the case of dispersal-limited species (Hannah *et al.* 2016). The challenge remains in identifying which reserves remain effective in meeting conservation targets (Hamann and Aitken 2013) and identifying climate-refugias that will meet conservation targets into the future (Keppel *et al.* 2012, 2015; Hannah *et al.* 2014).

Second, there is a need to identify the key spatial components of a species range (populations) that are critical genetic resources for the long term survival of a species. This is of particular concern for dispersal-limited species, such as forest trees, that are less likely to keep pace with the velocity of

current and future climate change (Loarie *et al.* 2009; Gonzalez *et al.* 2012). Identifying components of a species distribution that are likely to be buffered from the effects of climate change will be critical to guide the *in situ* management of these key genetic resources. Further, the identification of components of a species distribution that are exposed to maladaptation under climate change will be important in guiding *ex situ* conservation efforts, albeit through the establishment of insurance populations (e.g. in favourable environments within or outside of the species current distribution) or as intense collection of seed for long-term storage in seedbanks (Schoen and Brown 2001).

1.2.3 Using niche models to support conservation decisions

Predictive models provide valuable insights into the potential impact climate change may impose on species distributions. Indeed, habitat suitability models (also referred to as species distribution models or ecological niche models) derived by modelling the relationship between a species occurrence and environment (such as climate) have gained increased popularity among conservation scientists, with hundreds of published papers describing the potential impact climate change may have on a species using these techniques (Chapman *et al.* 2014). For example, they have been used to: (i) gain insights into past biogeographical patterns of species to better understand potential future impacts (Mokany *et al.* 2016) (ii) demonstrate the potential loss and gain of suitable habitat under future climate change for flora found in mountainous regions across Europe (Engler *et al.* 2011) and in diverse habitats within Australia (Butt *et al.* 2013), and (iii) determine the potential impact climate change may have on phylogenetic diversity (Thuiller *et al.* 2011; Zhang *et al.* 2015; Gonzalez-Orozco *et al.* 2016).

Habitat suitability models draw on the assumptions of Hutchinson's (1957) 'fundamental niche'. In the absence of competition, the fundamental niche is the combination of biotic and abiotic components of the environment that define the multivariate hyper-space that permits a species to survive and reproduce indefinitely (Hutchinson 1957). If competition is accounted for, the model

represents the 'realised niche' which is conceptually a hyper-volume within the fundamental niche, where the species being studied has a competitive advantage over all other species (Hutchinson 1957). Indeed, habitat suitability models based on occurrence-only data could be argued to maintain signals of past competition (i.e. 'ghost of competition past' – Connell 1980), and likely represent something close to the realised niche (Wisz *et al.* 2013).

There are assumptions and limitations to habitat suitability models (Pearson and Dawson 2003; Sinclair *et al.* 2010; Araujo and Peterson 2012) that require a brief appreciation before their interpretation. First, they assume the environment, particularly the climate, governs the spatial distribution of a species. While it is likely that climate is often a key driver that shapes the distribution limits of species (Davidson and Reid 1985; Davis and Shaw 2001) and can indeed often predict the distribution of a species, it is also possible that climate has little to do with shaping distribution margins despite providing a reasonably convincing model (Lozier *et al.* 2009). Second, the models assume species are in equilibrium with their environment. That is, they occupy all available suitable habitat. This assumption is unlikely to be met given that most forest tree species are unable to occupy particular habitats due to dispersal limitations (e.g. slow migration out of glacial refugia – McKinnon *et al.* 2004). Additionally, given the longevity of forest tree species (Petit and Hampe 2006), it is also possible that they are currently persisting in habitats that are sub-optimal for new recruits which could lead to models that over-predict suitable habitat (Sinclair *et al*. 2010). Third, uneven spatial and environmental sampling may lead to a biased model. Spatial bias can arise due to the uneven sampling of a species, for example, along a walking track or road and is explicit in most natural resource databases (Varela *et al.* 2014). This bias in turn can lead to the overrepresentation of a particular environment (Anderson and Gonzalez 2011), resulting in a model that fits the spatial bias rather than representing the species, which limits the wider application of the model (Araújo and Guisan 2006). Fourth, the model usually ignores the spatial structuring of genetic

variation within species that has resulted from local adaptations through evolutionary time. Rather than treating the species as a homogenous gene pool, Ikeda *et al.* (2016) showed that the partitioning of genetically distinct groups indeed provided a more accurate model than one based only on traditional methods (i.e. a model based on environmental data with no population structure).

While the limitations of habitat suitability models are well-known, they nevertheless provide conservation managers an additional tool to support the short term and long term conservation planning of a species. Indeed, they have been used to evaluate the effectiveness of reserves (Hamann and Aitken 2013), identify future climate refugia (Keppel *et al.* 2015; Mokany *et al.* 2016), and assist in the translocations of dispersal-limited species, such as forest trees (Gray *et al.* 2011; Gray and Hamann 2013). However, many studies neglect to differentiate between reductions in suitable habitat and the underlying proportion of a species distribution that either remains within this modelled space or that may be exposed to the potential risk of maladaptation. Indeed, reporting only modelled changes in suitable habitat can lead to over-predictions of a species exposure under future climate change (e.g. Gonzalez-Orozco *et al.* 2016) that can impinge on formulating effective management plans. There is now a need to better understand the relationship between the contraction and stability of modelled suitable habitat and the proportion of a species distribution maintained within suitable habitat.

1.3 Ecological restoration as a key conservation strategy

Ecological restoration will play a pivotal role in mitigating the loss of biodiversity under future climate change, and indeed the value of ecological restoration as a conservation strategy in the face of climate change has been well recognised (Jordan *et al.* 1988; Young 2000; Bennett *et al.* 2009). Ecological restoration is "*the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed*" (McDonald *et al.* 2016). Many countries are heavily investing in

restoring forest ecosystems through initiatives such as the Bonn Challenge, which has targeted 350 million hectares of degraded forests for restoration by 2030 (Verdone and Seidl 2017). Indeed, this ambitious target is expected to generate a net benefit of up to US$9 trillion (Verdon and Seild 2017).

Traditionally, the ecological restoration of forest ecosystems has followed the long-standing 'local-is-best' approach, where germplasm (i.e. seed) is sourced from locally occurring species following a 'local provenancing' strategy. Here, a 'provenance' is defined as the geographic and environmental location of a population that is used to describe the genetic material (individuals) from that location (Rehfeldt *et al.* 1999). The local provenancing approach has gained wide acceptance among restoration ecologists (Hancock and Hughes 2012) for a number of reasons. First, a local provenancing strategy maintains the genetic integrity of the provenance (McKay *et al.* 2001; O'Brien *et al.* 2007) and limits the potential of outbreeding depression caused by the disruption of locally adapted gene complexes (Costa e Silva *et al.* 2012; Hufford *et al.* 2012) and heterosis (increased fitness of the hybrid product - Costa e Silva *et al.* 2014). Second, it maintains co-evolutionary history that has evolved among plants (Grady *et al.* 2016) and the extended community of the ecosystem (Whitham *et al.* 2006). Third, it limits the risk of maladaptation and increases the chances of establishment success (Grady *et al.* 2015). Nevertheless, the key assumption of local provenancing is that the local provenance is optimally adapted to its biotic and abiotic environment, whereby local genotypes have a fitness advantage over non-local genotypes.

Evidence for local adaptation to home-site environmental variation has traditionally been obtained through the monitoring of provenance performance in common garden field trials. Indeed, the 'gold standard' in detecting local adaptation remains the establishment of reciprocal transplant experiments, where pairwise local and non-local genotypes are replicated and compared across selective gradients in 'home-site *versus* foreign' designs (Kawecki and Ebert 2004; Blanquart *et al.* 2013). There is a rich history of provenance testing in widespread forest tree species planted along

elevation and climate gradients (Aitken and Bemmels 2015), which have been retrospectively used to study and demonstrate local adaptation (Matyas 1996; Rehfeldt *et al.* 1999; Hereford 2009; Wang *et al.* 2010; Gray *et al.* 2016). There is little doubt that plants perceive and adapt to their micro-climate (McKay *et al.* 2001; Hall *et al.* 2007), macro-climate (Rehfeldt *et al.* 1999; St Clair *et al.* 2005; Gauli *et al.* 2015), soil type (Sambatti and Rice 2006; Wright 2007), soil biota (Sherrard and Maherali 2012), and natural enemies (O'Reilly-Wapstra *et al.* 2004; Garrido *et al.* 2012), suggesting that local adaption may be the rule rather than the exception. Indeed, Hereford (2009) and Leimu and Fischer (2008) showed that in 71% of cases reviewed, the local provenance outperformed the non-local provenances when planted at their home-site.

In the Anthropocene era, where global change (land-use change and climate change) is ubiquitous across forest ecosystems, the reliance on the traditional local provenancing strategy for ecological restoration has been increasing challenged (Jones 2013a). First, through intense land-use change, such as land clearing for agriculture, it is likely that most of the remnant forest ecosystems have transitioned into either a 'hybrid' state which maintains both a historical component as well as a novel component, or a 'novel' state which has little to no historical component maintained (Hobbs *et al.* 2009). Indeed, changes in land management practices have altered various processes, functions, and structures of forest ecosystems, including the cycling of nutrients, functional roles of the soil microbiota, and above- and below-ground biodiversity (de Vries *et al.* 2013; Bardgett and van der Putten 2014; Paula *et al.* 2014; Groppo *et al.* 2015; Newbold *et al.* 2015; Smith *et al.* 2016). In such cases, it is likely that the ecosystem has surpassed critical thresholds where it is difficult to near impossible to restore the ecosystem to a previous state using traditional restoration practices (Hobbs *et al.* 2014). Second, increased fragmentation of remnant vegetation through land-use change has likely decreased the genetic diversity within provenances (Young *et al.* 1996) due to altered pollinator patterns, increased inbreeding, and reduced effective population sizes (Ellstrand and Elam

1993; Broadhurst *et al.* 2015). While genetic diversity may be maintained in long-lived species (Hamrick 2004) and species with effective gene flow vectors (Breed *et al.* 2013), using genetically depauperate seed may diminish adaptive abilities to future environmental flux (Jump and Penuelas 2005) and increases the economic costs associated with seed collections (Broadhurst *et al.* 2008). Third, the increased likelihood of inbreeding within fragmented remnant vegetation is also likely to lower the relative fitness of the local provenance through time due to the expression of inbreeding depression (Hardner and Potts 1995). Fourth, climate change is likely to shift the mean of the selective regimes that have historically shaped local adaptations, potentially increasing the maladaptation of local genotypes under novel environments. Indeed, the northward displacement of selection regimes acting on *Chamaecrista fasiculata* is expected to result in differential favouring of provenance trait means (Etterson 2004).

In light of the abovementioned issues surrounding traditional ecological restoration practices, multiple alternative seed sourcing strategies (Figure 1.3) have been proposed to supplement local seed collections with non-local seed to bolster genetic diversity and improve the 'climate-resilience' of the restoration plantings and ecosystems into the future. Here, climate-resilience is conceptually similar to 'ecological-resilience' (Angeler and Allen 2016) and is defined as the ability of an ecosystem to respond and change its processes and structure in response to a change in the climate. The alternative seed sourcing strategies are conceptually special cases of assisted gene flow within a species distribution (Aitken and Whitlock 2013), and each are broadly reviewed below.

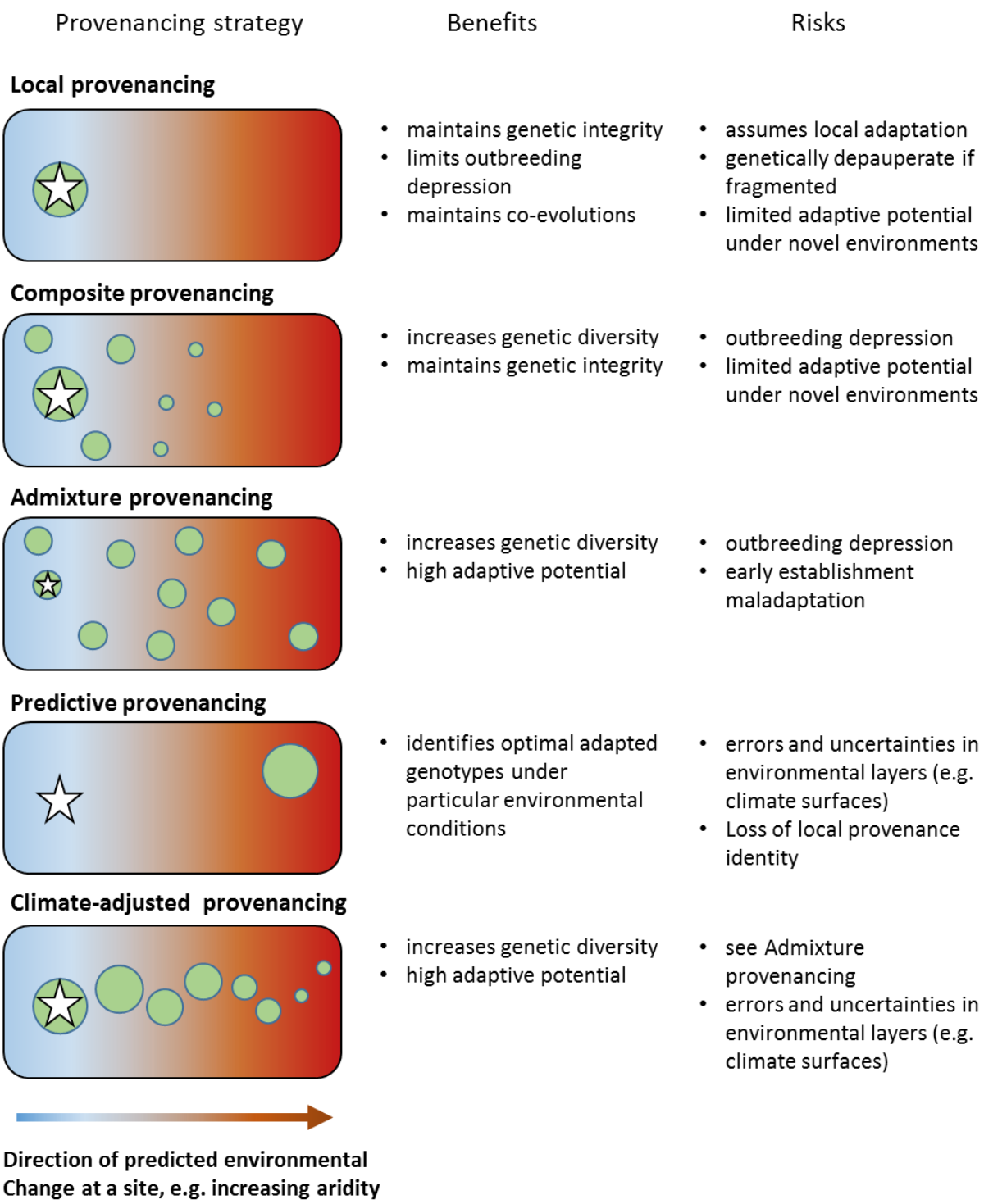


Figure 1.3. Provenancing strategies used in ecological restoration of an ecosystem, as well as the benefits and risks associated with each strategy. Shown is a conceptual depiction of each strategy (modified from Prober *et al.* 2015) applied across a hypothetical landscape of increasing aridity. The site being restored is identified with the white star symbol and the green circles correspond to native provenances across the species distribution range. The size of the circle indicates the relative sampling effort.

Composite provenancing. Attempts to minimise the effects of habitat fragmentation by mimicking the natural gene flow among provenances by supplementing local seed with seed from multiple non-local provenances within gene flow distance (Figure 1.3; Broadhurst *et al.* 2008). While there is an increased chance of outbreeding depression with this strategy (Hufford *et al.* 2012), the relative risk are belived to be overstated (Frankham *et al*. 2011). Nonetheless,this approach can increase the genetic diversity of the pooled seed collections but this may not necessarily increase potential adaptability to future environments created by global warming (Sgrò *et al.* 2011; Breed *et al.* 2013).

Admixture provenancing. Attempts to maximise the adaptive potential of the restoration planting by supplementing the local seed collections with 'holistic' seed collections across a species' natural distribution (Figure 1.3; Breed *et al.* 2013). This approach is particularly useful if the direction and/or magnitude of projected climate change are unknown, as genetic diversity is pooled from across the entire range of a species to maximise the adaptability and climate-resilience of the plantings (Breed *et al.* 2013).

Predictive provenancing. Attempts to identify the best provenances using long-term experiments to understand how provenance performance in key traits (such as survival and growth) relates to the home-site climate (where the seed originated). These relationships are then used to derive reaction norms (e.g. Wang *et al.* 2010) to identify provenances that are optimally adapted to current or future climates of a restoration site (Figure 1.3; Crowe and Parker 2008; Sgrò *et al.* 2011). However, the long-term experiments required for this are rarely available for forest species, and indeed are often only available for commercially important forestry species (e.g. Gray and Hamann 2011; Dutkowski and Potts 2012).

Climate-adjusted provenancing. Attempts to maximise the adaptability and climate-resilience of the restoration plantings by pooling local and non-local seed collections along the gradient of change, i.e. climate change (Figure 1.3; Prober *et al.* 2015). The premise of this strategy relies on two assumptions. First, it assumes the genetic variation among provenances has to some extent been

shaped by the climate. Second, it assumes that non-local provenances matched to future climates of a restoration site can successfully establish under current climate conditions (Grady *et al.* 2015). Thus, the general extent and scale of local adaptation among provenances of a species and the transfer limits requires further study, and is a core focus of this thesis.

1.4 Ecological restoration of Australian *Eucalyptus* woodlands: case of the Tasmanian Midlands

1.4.1 Defining the Australian eucalypt woodland ecotype

Eucalypt woodlands have an iconic place in the Australia landscape. A 'woodland' is a sparse forest ecosystem which has widely spaced trees growing to 10-30 m tall and a relatively open canopy, with crowns that overlap by less than 30% (Yates and Hobbs 1997; Duncan 2005). Woodlands occur across a variety of environments, ranging from summer rainfall dominated sub-tropical regions of southern Queensland to Mediterranean dominated climates in south-west and southern Australia (Moore 1970). They are most prevalent on drier sites that experience a mean annual rainfall between 200-800 mm, and often form a transitional zone between wet sclerophyllous forests and shrubland/grassland ecosystems (Beadle 1981). To a lesser extent, woodlands also occur in higher rainfall areas, such as the sub-alpine woodland regions of Tasmania.

The pre-European floristic composition of most eucalypt woodlands in Australia is poorly understood as a result of extensive land conversion for agriculture (Prober and Brown 1994; Prober and Thiele 2005). However, studies of relatively intact remnant woodlands suggest that floristic composition and structure are strongly dependent on latitude and environmental factors including climate, soil, and disturbance regimes such as drought and fire history (Trémont and McIntyre 1994; Prober and Brown 1994; Hamilton 2001; Duncan 2005). Thus, eucalypt woodlands can have a patchy understory consisting of shrub species (shrubby woodlands) or grass species (grassy

woodland). Shrubby woodlands are often extensions of adjacent forest that extend into less favourable, drier environments and generally maintain floristically similar species (Auslig 1990). This woodland type commonly consists of members from the Cupressaceae, Casuarinaceae, Ericaceae, Fabaceae, Mimosaceae, and Myrtaceae families (Hobbs and Yates 2000). Grassy woodlands, on the other hand, generally occur on more fertile substrates that are subjected to periodic flooding (Auslig 1990; Trémont and McIntyre 1994). Members of the Poaceae family generally dominate the understory of these woodlands, however, members of the Asteraceae, Asparagaceae, Fabaceae, Liliaceae, Orchidaceae, Juncaceae and Cyperaceae are also common (Trémont and McIntyre 1994; Duncan 2005).

1.4.2 Degradation across Australian eucalypt woodlands

Following European settlement, eucalypt woodlands have experienced the widest decline of any forest type in Australia. It has been estimated that a total of 500 000 km^2 (or 34%) of eucalypt woodlands have been converted to agricultural or other vegetation types through anthropogenic processes (e.g. land clearing, invasive species, climate change; Auslig 1990; Beeton *et al.* 2006). Most of this land conversion has disproportionately occurred in woodlands that occupy more fertile substrates which are amenable to agriculture (Hobbs and Yates 2000). For example, in the wheatbelt region of eastern and western Australia, it has been estimated that 95% of remnant woodlands have been modified or converted to agriculture (Hobbs and Yates 2000; Cox *et al.* 2001).

Continued clearing of remnant patches can further exacerbate stresses already imposed on these woodland ecosystems. First, the replacement of deep-rooted woodland vegetation, such as eucalypts, with shallow-rooted agricultural crops has led to increased salinity due to altered water cycles that result in the rising water tables that mobilises salts previously stored in the soil profile (Clarke *et al.* 2002; Bui 2013). Indeed, it is estimated that 5.7 million hectares are either at risk or affected by

dryland salinity, with the majority of affected sites occurring within the south-eastern and south-western wheatbelt regions of Australia and the Tasmanian Midlands (Beeton *et al.* 2006). Second, land-use change has resulted in the nutrient enrichment of woodlands following applications of fertilisers that either enter the system directly by run-off, or leaching from surrounding farmland, or through livestock (Yates and Hobbs 1997; Close *et al.* 2008). Third, livestock grazing in fragmented woodlands has had profound effects on the eco-physiological processes in these ecosystems, not only altering natural nutrient fluxes but also soil properties such as compaction and water infiltration (Yates and Hobbs 1997; Hobbs and Yates 2000). Indeed, altered soil characteristics has been suggested as a limiting factor for early growth of *Eucalyptus salmonophloia* (Yates *et al.* 1995).

Climate-induced dieback is further accelerating the human-induced chronic decline of Australia's eucalypt woodlands (Jurskis 2005). Extreme temperature and drought stress has been attributed to widespread episodes of woodland dieback (Fensham *et al.* 2009; Allen *et al.* 2010), which are predicted to be further exacerbated under future climate change (Allen *et al.* 2010). Thus, there is now a great need to restore, buffer, and link woodlands across the landscape to increase their climate-resilience under future environmental flux.

1.4.3 Restoring the Australian eucalypt woodland: case of the Tasmanian Midlands

The Tasmanian Midlands was once floristically diverse with large expanses of eucalypt woodlands across this warm, drought-prone landscape (Fensham 1989). However, following European settlement, widespread land conversions for agriculture resulted in the loss of 83% of native vegetation throughout the Midlands (Fensham and Kirkpatrick 1989), with an estimated 90% reduction in area of the grassy woodland ecosystems (Kirkpatrick *et al.* 1988) dominated by *Eucalyptus amygdalina*, *E. pauciflora*, *E. ovata*, and *E. viminalis* (Fensham 1989). Anthropogenic influences (discussed above) are prolific throughout these systems and are the leading drivers of rural

tree decline across Tasmania (Close and Davidson 2004; Davidson *et al.* 2007). This has led to the listing of these woodland ecosystems as 'Threatened Community Types' under the *National Conversation Act* 2002.

Eucalypts are important components of forest ecosystem structure and composition (Fairman *et al.* 2016) and this thesis focuses on the large, landscape-level restoration projects currently underway in the Tasmanian Midlands (e.g. Bailey *et al.* 2013). These restoration projects are aimed at restoring and linking remnant eucalypt woodland patches across the agricultural matrix to improve connectivity for both animal and plant dispersal, buffer remnant vegetation against current and future climate change, and conserve and restore ecosystem functioning and services (Whitten *et al.* 2011; Bailey *et al.* 2013).

1.5 Study system

1.5.1 The Tasmanian eucalypts

Eucalyptus (Myrtaceae) is a hyper-diverse group of species from three genera (*Eucalyptus*, *Corymbia*, *Angophora*) with nearly 900 recognised species that dominate most of the forest ecosystems across the Australian continent (Slee *et al.* 2006; Nicolle 2015). Most eucalypts are endemic to Australia, with the exception of six species endemic to islands north of the Australian continent. The island of Tasmania represents the southern-most extent of eucalypts in Australia, where there is a rich eucalypt flora with 30 native species from two subgenera (*Eucalyptus* and *Symphyomyrtus*). Tasmania forms one of the 14 centres of *Eucalyptus* endemism (González-Orozco *et al.* 2014), where 60% of the islands species are endemic (Williams and Potts 1996). *Eucalyptus* are often the dominant tree of sclerophyllous ecosystems on the island, from wet forests that support species of high economic value for forestry (i.e. *E. delegatensis*, *E. obliqua*, *E. regnans* and *E. globulus*; Baker and Read 2011; Doughty 2000) to dry mallee (i.e. multi-stem shrubby habit) forests

that are prone to drought (i.e. *E. risdonii*). The eucalypts of Tasmania occupy a wide-range of altitudes across the complex, heterogeneous landscape of the island. They occurr from near sea-level to the sub-alpine treeline, where they range in habit from the world's tallest angiosperm (*E. regnans*; Grattapaglia *et al*. 2012) to a small, stunted alpine shrub (*E. vernicosa*; McGowen *et al.* 2001).

1.5.2 Choice of species for this thesis: Eucalyptus ovata

The experimental component of this thesis focuses on the woodland dominant, *Eucalyptus ovata* (Labill.), which is a species currently targeted for the ecological restoration of grassy woodlands across the Midlands of Tasmania. *Eucalyptus ovata*, commonly known as black swamp gum in Tasmania, is a member of the series *Foveolatae* (section *Maidenaria*, subgenus *Symphyomyrtus*), which is a comparably large series made up of 13 species (Nicolle 2015). Some of the earliest work on *Foveolatae* investigated the seedling characteristics of *E. ovata* and *E. brookeriana* (Clucas and Ladiges 1979; Ladiges *et al.* 1981), which was spurred by the description of *E. brookeriana* (Gray 1979). The adult form of *E. ovata* and *E. brookeriana* are often indistinguishable, however, they differ markedly in their seedling traits, with the mainland *E. brookeriana* seedling phenotype tending to have square stems with discolorous leaves (i.e. leaves with different coloured upper and lower surfaces) that are cordate with short petioles (Ladiges *et al.* 1981). The Tasmanian *E. brookeriana* seedling phenotype is noticeably different from the mainland phenotype, and tends to be nearly intermediate with the *E. ovata* seedling phenotype (Ladiges *et al*. 1981). Nevertheless, analysis of volatile leaf oils clearly separated these two species, with *E. ovata* producing more complex leaf oils (Brooker and Lassak 1981) which was further supported by Li *et al.* (1996). Since this early work, two subspecies of *Eucalyptus ovata* have been described, with subsp. *ovata* distinguished from subsp. *grandiflora* by its comparably smaller leaves and fruits (Nicolle 2006a).

Eucalyptus ovata subsp. *ovata* (hereafter abbreviated to *E. ovata*) is the more widespread of the two subspecies, and naturally occurs across the wetter lowlands of south-eastern Australia. Its geographic range extends across most of eastern and north-western Tasmania and is commonly found across the southern half of Victoria, with its distribution on mainland Australia reaching as far north as Bowral in New South Wales and as far west as South Australia where it is common on Kangaroo Island (Nicolle 2006a). *Eucalyptus ovata* grows across a diverse climatic range, with mean annual precipitation ranging from 541 mm to 1208 mm and mean annual temperature ranging from 9.4 ˚C to 14.8 ˚C. The mainland distribution of *E. ovata* is on average exposed to slightly warmer temperatures (mainland: 13.4 ˚C; Tasmania: 11.7 ˚C) but tend to occupy very similar precipitation zones (mainland: 809 mm; Tasmania: 824 mm). Like most of the *Foveolatae* species, *E. ovata* grows on poorly drained substrates that are prone to periodic floods. Nevertheless, *E. ovata* can also occur on drier sites where topographic depressions (i.e. undulating coastal regions and valley floors) collect water (Clucas and Ladiges 1979; Williams and Potts 1996; Nicolle 2006).

In Tasmania, *E. ovata* naturally occurs from near sea level (7 m) to 662 m above sea level, and occasionally extends as far up as 750 m (e.g. the edge of Woods Lake on the eastern Central Plateau), where it is replaced by *E. rodwayii* and *E. gunnii* on frost prone sites (Kirkpatrick and Gibson 1999). *Eucalyptus ovata* is the dominant tree of dry, grassy-shrubby woodlands in Tasmania (Figure 1.4; Fensham 1989), and often forms mixed stands with *E. amygdalina*, *E. pauciflora*, and *E. viminalis* as substrate drainage improves (Williams and Potts 1996). This species is rarely a dominant of well-drained wet sclerophyll forests and is often miss-identified as *E. brookeriana* (see above), especially in the north-western distribution of *E. ovata* (Williams and Potts 1996). *Eucalyptus ovata* grows as a short mallee on coastal and exposed sites but can reach heights of up to 30 m at more wet-prone sites (Clucas and Ladiges 1979; Williams and Potts 1996).

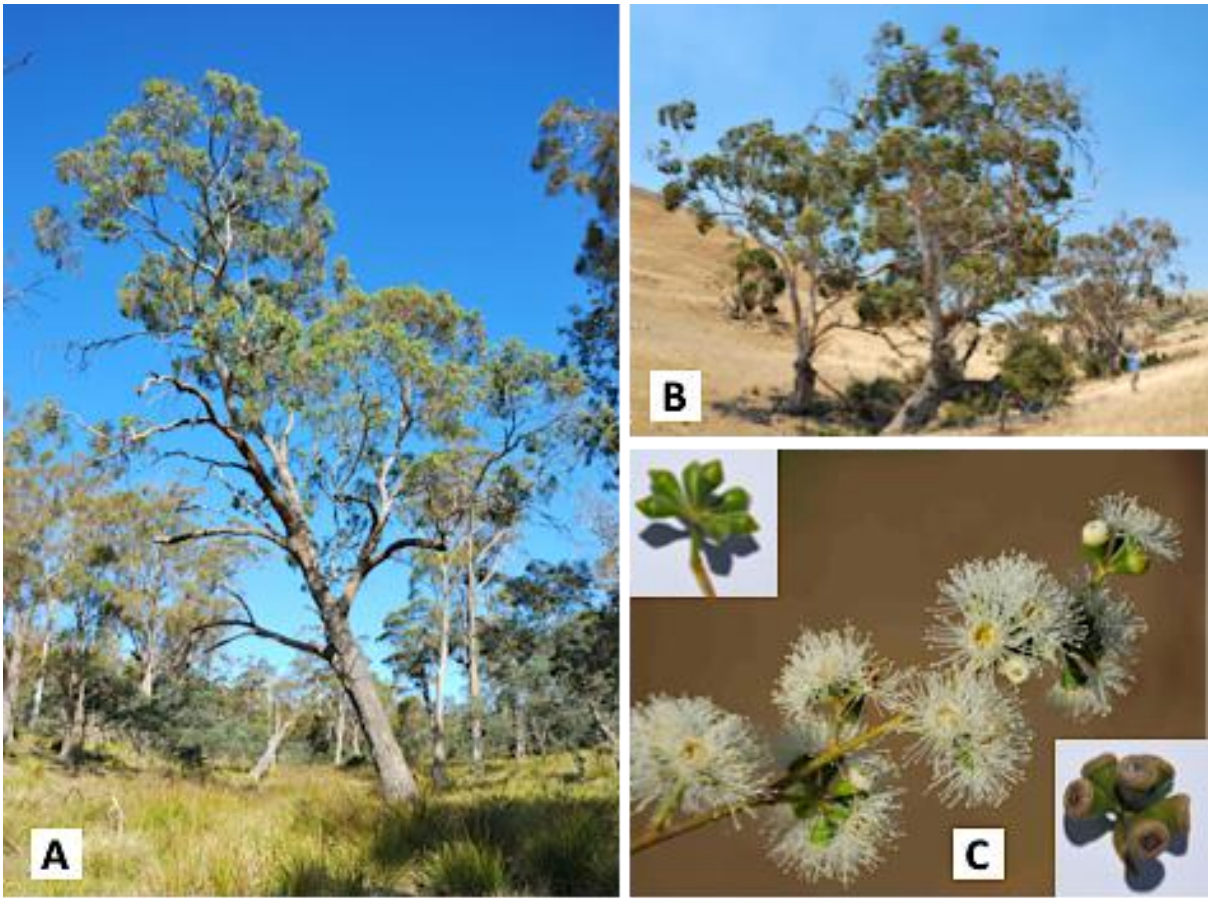


Figure 1.4. Panel A shows the typical grassy-sedgy woodland that is dominated by *E. ovata* (in centre foreground) in the undulating hills surrounding Ross in the northern Tasmanian Midlands. Panel B shows a typical fragmented and degraded *E. ovata* woodland near Hamilton in the southern Tasmanian Midlands. Panel C shows a branch of *E. ovata* laden with flowering buds, with a typical seven-fruit umbel of *E. ovata* showing the buds in the top-left and maturing capsules in the bottom-right. (Photos: P A. Harrison).

1.6 Thesis structure

This thesis provides a methodological approach to integrate climate change projections into the conservation and ecological restoration of woodland forest ecosystems. It uses habitat suitability models to explore the impact of climate change on the diverse eucalypt flora of Tasmania, and explores the climate-adjusted provenancing strategy for the ecological restoration of *E. ovata* woodlands by understand the projected impact on climate change and the extent and scale of local adaptation across the distribution of this species. Chapters 2 through to 6 of this thesis are experimental chapters that have been written in the format of stand-alone papers in preparation for publication. Chapter 2 develops some of the first habitat suitability models for the Tasmanian

eucalypt flora and explores the effectiveness of current reserve systems under future climate change scenarios. Chapter 3 uses the developed habitat suitability models to evaluate the suitability of current target eucalypt species for restoration under future climates as well as identify potential candidate species that may not be locally occuring but may provide alternative functional equivilents to restore ecosystem services. Chapter 4 provides a methodological framework to guide provenance choice of candidate species for ecological restoration, focusing on current target eucalypt species of the Tasmanian Midlands. Chapters 5 and 6 focus specifically on populations of *Eucalyptus ovata* in Tasmania, with the goal of understanding germination requirements, the extent of local adaptation and the association between local adaptation and climate, and to experimentally validate some of the assumptions raised in Chapters 2, 3 and 4. Chapter 7 provides a general synthesis of the work undertaken in this thesis and discusses the key findings and conclusions, as well as points to outstanding issues that require further research. A summary of the content and specific aims/questions being addressed by each experimental chapter is provided below.

1.6.1 Chapter 2: Guiding in situ conservation through identification of populations vulnerable to climate change

This chapter explores the potential impact of future climate change on the eucalypt flora of Tasmania using habitat suitability models derived using the machine learning algorithm 'random forest'. It presents a new approach to determine a species exposure by quantifying the proportion of its distribution at risk of maladaptation as modelled suitable habitat shifts through time. This chapter provides species- and diversity-level maps describing the predicted shift in suitable habitat, and tests whether attributes of the species can predict its future susceptibility to climate change maladaptation. In doing so, this chapter specifically addresses the following research questions:

1. What components of the current distribution of each species are likely to become maladapted under future climate change scenarios?
2. What species attributes predict susceptibility to maladaptation under climate change?

3. How climate-resilient is the current reserve estate in Tasmania and do they encompass populations which are unlikely to be exposed to climate maladaptation, under a no or limited dispersal scenario?

1.6.2 Chapter 3: Planning for emerging novel ecosystems using habitat suitability models: the case for the Midlands of Tasmania, Australia

While niche models have been used extensively in conservation planning, there has been relatively little uptake of these methods to help guide species choice in ecological restoration. Here, this chapter provides a methodological approach to incorporate niche models into species choice decisions for ecological restoration by developing a criteria-based framework that integrates the habitat suitability models derived in Chapter 2 with an assessment of susceptibility to track the spatial and temporal change in the choice of candidate species for ecological restoration under future climates. This framework is demonstrated using the Tasmanian Midlands restoration region as a case study. This chapter addresses the extent of the traditional 'local-is-best' at the species-level and models how species choice may change into the future under current and future novel environments.

1.6.3 Chapter 4: Integrating climate change and habitat fragmentation to identify candidate seed sources for ecological restoration

This chapter follows on from Chapter 3 and explores where in the distribution of a candidate species to collect the best seed sources that are suitable for future climates. This chapter develops a framework to implement the climate-adjusted provenancing strategy while accounting for potential inbreeding in fragmented forests, and is implemented through the R package PUCA (Provenancing Using Climate Analogues). This framework is demonstrated using two sites (Ross and Cressy) within the Tasmanian Midlands as case studies, where eucalypt woodland ecosystems are currently being restored using six key restoration species

1.6.4 Chapter 5: Provenance and seed mass determines the seed germination success of Eucalyptus ovata (Myrtaceae)

This chapter explores the factors that affect seed germination using multiple provenances of *E. ovata*. Given the altitudinal range on this species, it was hypothesised that high altitudinal provenances of *E. ovata* would require a wet, cold stratification to enhance germination success. This was tested using multiple sites across the natural distribution of *E. ovata* in Tasmania, were each site had a sampled low and high altitude provenance.

1.6.5 Chapter 6: Using signals of selection in functional traits to model spatiotemporal change in the selection surface

This chapter explores a method to 'fast track' the identification of key climate factors shaping adaptive variation within a species using a quantitative genetic model. It develops a two-stage framework to firstly identify seedling traits that show independent signals of putative divergent selection, then secondly derives an adaptively-enriched genetic space (using the traits under divergent selection) that is climate-aligned to develop a climate selection surface. This framework is empirically tested using *E. ovata* progeny trials established in the glasshouse and field. This chapter establishes the procedures for the testing of key assumptions raised in Chapter 4, and assumptions made by the climate-adjusted provenancing strategy. It specifically addresses the following research questions:

1. Is adaptive variation within *E. ovata* shaped by variation in climate?
2. How will future climate change interact with adaptive variation to reshape the selective surface of *E. ovata* in Tasmania?
3. Does differential climate adaptation impact early establishment success of planted seedlings following the translocation of provenances from diverse home-site climates into a restoration planting site?

Chapter 2: Guiding *in situ* conservation through identification of populations vulnerable to climate change

Abstract

Global climate change will negatively impact major components of the world's biodiversity over the next century, and there is an increasing need for strategies and tools to guide species conservation and management. Habitat suitability models have gained increasing popularity with practitioners over the past decade, and we here demonstrate how such models can potentially identify populations least susceptible to climate change that may be important for species long-term persistence. Using Random Forest models and the diverse *Eucalyptus* flora of the island of Tasmania, Australia, we evaluate whether: (i) populations are likely to be outside their current modelled suitable habitat under future climate change and thus at risk of future maladaptation, (ii) whether susceptibility to climate change is predictable, and (iii) whether current reserve systems are likely 'climate refugias'. Three key findings emerged from this study. Firstly, the models predicted large extents of currently suitable climate habitat will be lost by the end of this century, exposing populations to potential risk of maladaptation. Secondly, there was a certain predictability to the risk of maladaptation faced by a species under future climate change. Subalpine species were most susceptible, however, this susceptibility was not linked to a species evolutionary history. Lastly, while hotspots of eucalypt diversity may non-uniformly erode by the end of this century, the current reserve systems maintained large components of this diversity that were not at risk of climate maladaptation into the future. We discuss the potential capacity for species such as eucalypts to persist outside modelled suitable habitat, but highlight how such populations may face heightened extinction risks through stochastic processes. Strategies to conserve populations into the future will need to be dynamic to maximise gene pool conservation and capitalise on opportunities to capture genetic resources, especially from populations predicted to be outside their current modelled suitable habitat under future climate change.

2.1 Introduction

Climate change is likely to be one of the greatest threats currently facing global biodiversity (Malcolm *et al.* 2006). As global emissions continue to track the 'worse-case' scenarios (Peters *et al.* 2012), notwithstanding a recent plateau in emissions (Jackson *et al.* 2016),and with little global mitigation occurring, the future impact of climate change may have serious consequences on biodiversity (Maclean and Wilson 2011; Bellard *et al.* 2012). Already there are examples of the negative impacts that current climate change is having on freshwater (Comte *et al.* 2013), marine (Poloczanska *et al.* 2016), and terrestrial (Allen *et al.* 2010; Descamps *et al.* 2016) ecosystems. There is now growing evidence that species are beginning to migrate to higher latitudes and elevations in response to current climate change (Thomas 2010; Chen *et al.* 2011; Feeley *et al.* 2013; Fisichelli *et al.* 2014; Serra-Diaz *et al.* 2016). However, dispersal-limited and sessile species may not be able to readily disperse into available habitats under climate change (Aitken *et al.* 2008; Zhu *et al.* 2012; Corlett and Westcott 2013) and such populations may be at a higher risk of extirpation.

Habitat suitability models (also known as species distribution models or ecological niche models) have been widely used to assess the vulnerability of species to maladaptation under future climate regimes (Guisan *et al.* 2013; Chapman *et al.* 2014). These models draw on ecological niche theory (Hutchinson 1957) and statistical relationships between the spatial distribution of a species and environmental variables to predict areas of suitable habitat. Suitable habitat is conceptually the combination of environmental factors that promote self-sustaining populations in the presence of competition (Hutchinson 1957). Despite the many known limitations of these species distribution models (Pearson and Dawson 2003; Sinclair *et al.* 2010; Araujo and Peterson 2012), they often provide the best-available predictions for conservation planning (Guisan *et al.* 2013; Hamann and Aitken 2013; but see Franklin 2013). For example, habitat suitability models have been increasingly used to guide the planning of *ex situ* translocation (assisted colonisation) and *in situ* translocation

(assisted migration) of populations identified at risk of extinction (Gray *et al.* 2011; McLane and Aitken 2012).

The exposure of species to future climate change has generally been inferred from the difference between the areas of modelled contemporary and future suitable habitat (Crossman *et al.* 2012). However, dispersal-limited species rarely fully occupy their modelled suitable habitat, and this appears to be the case for many forest species (Eriksson and Ehrlén 1992). For example, species may be confined to putative glacial refugias (e.g. *Eucalyptus cordata*, Harrison *et al.* 2014) or constrained by extinction-colonisation metapopulation dynamics (Hanski 1998). Accordingly, the loss of modelled suitable habitat may give an inflated impression of exposure that deviates markedly when considering the proportion of a species distribution (i.e. the habitat it actually occupies) that is contained within modelled suitable habitat. Furthermore, it can lead to an overly optimistic prediction on the effectiveness of current reserve systems under future climate change scenarios (Thomas *et al.* 2012). To overcome this, we propose a new approach where the exposure of a species to future climate change is quantified as the change in the proportion of its distribution contained within modelled suitable habitat. This approach allows explicit investigation of populations that may be at risk of future extirpation through maladaptation for *ex situ* conservation or alternatively the targeting of populations which are least vulnerable to maladaptation under future climate change for *in situ* conservation.

Here, we illustrate how this approach can inform *in situ* gene pool conservation efforts of the genus *Eucalyptus* on the island of Tasmania, Australia, by focusing on stable components of the species distribution under climate change. The eucalypts of Tasmania are an ideal study system as they have a deep evolutionary history on the island (McKinnon *et al.* 2004; Harrison *et al.* 2014), and are represented by endemic and non-endemic species with contrasting range sizes, in addition to

occupying a diversity of habitats from near sea level to the subalpine tree line (Williams and Potts 1996). This diversity allows us to test whether there is a predictable component to species risk of maladaptation to future climates. In this study our objectives were to evaluate: (i) what components of the current distribution of each species are outside modelled suitable habitat under future climate change scenarios and at a higher risk of maladapted; (ii) what species attributes predict susceptibility to maladaptation under climate change; and (iii) how climate-resilient is the current reserve system and whether these reserves include populations which are unlikely to be exposed to the risk of climate maladaptation under no or limited dispersal scenarios.

2.2 Material and methods

2.2.1 Study region

Our study region was the island of Tasmania (64, 519 km^2 in surface area) off the south-east coast of mainland Australia (*c.* 39°S-43.5°S, 143.5°E-149°E; Figure 2.1). The island has a cool temperate climate that is influenced by the surrounding oceans. Mean annual temperatures range between 3.9 °C on the Central Plateau to 14.5 °C in the north-east, with mean maximum summer temperatures being most extreme in the Midlands of Tasmania (24.7 °C). Precipitation tends to be seasonal (winter months) with a strong longitudinal rainfall gradient running west to east across the island. The west-coast of Tasmania receives >3000 mm $year^{-1}$ compared to areas of eastern Tasmania that receives <500 mm $year^{-1}$. Most soils are highly-weathered and nutrient deficient, but there are more fertile pockets of basalt and dolerite parent material. The combination of generally infertile soils and a topographically complex landscape results in a mosaic of diverse vegetation communities, from grasslands/woodlands in arid areas to ancient rainforests in higher-rainfall areas. This mosaic of diverse vegetation on the island of Tasmania has high conservation value (i.e. palaeoendemic species, Jordan *et al.* 2016) that is predicated to be at risk under future climates (Williamson *et al.* 2014; Worth *et al.* 2014; Mokany *et al.* 2016).

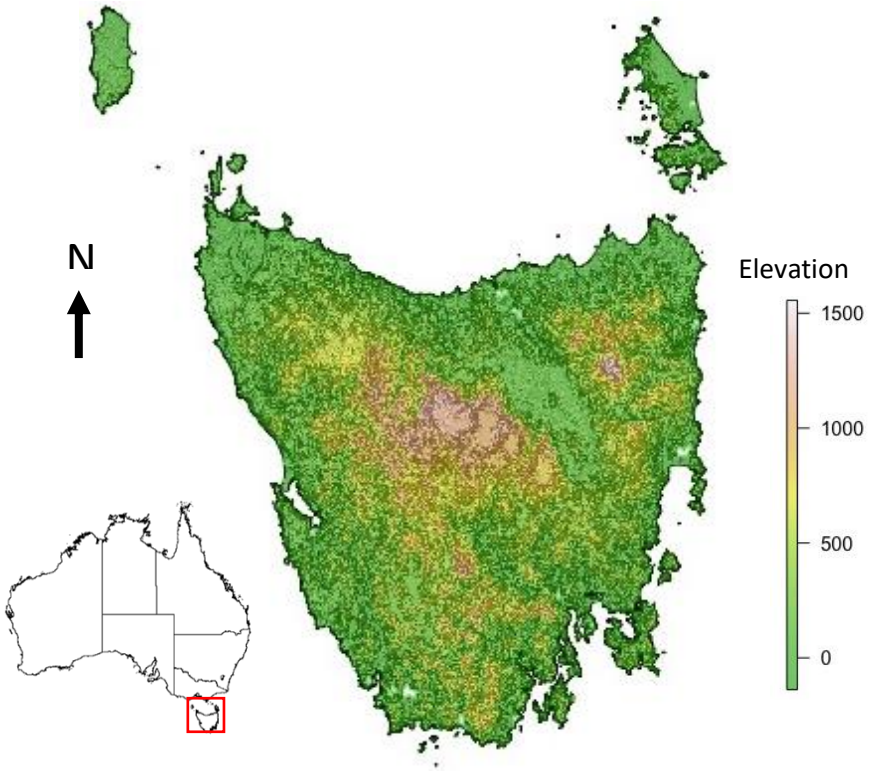


Figure 2.1. The geographic location of Tasmania (red box) relative to the mainland continent of Australia. The rugged topography of Tasmania has been shown by overlaying the 9 second Australian bathymetric and topographic grid (Geoscience Australia; http://www.ga.gov.au) on a hillshade (calculated using slope and aspect), with the colour gradient running for low elevation (dark green) to high elevation (light brown).

2.2.2 Study species and occurrence data

Tasmania has a rich eucalypt flora with 30 native species from two subgenera (*Eucalyptus* and *Symphyomyrtus*). Tasmania forms one of the 14 centres of *Eucalyptus* endemism (González-Orozco *et al.* 2014), with 60% of species endemic to Tasmania (Williams and Potts 1996). *Eucalyptus* are often the dominant tree of sclerophyllous ecosystems from wet forests that support species of high economic value for forestry (i.e. *E. delegatensis*, *E. obliqua*, *E. regnans* and *E. globulus*; Doughty 2000; Baker and Read 2011) to dry forests that are prone to drought (i.e. *E. risdonii*). The eucalypts of Tasmania occupy a wide-range of altitudes from near sea-level to the sub-alpine tree line, where they range in habit from a small, stunted alpine shrub (*E. vernicosa*; McGowen 2001) to the world's tallest angiosperm (*E. regnans*; Grattapaglia *et al.* 2012).

Tasmania represents the southern-most distribution range for eucalypts in Australia. While it is assumed that the habitat suitability models capture the full environment space of a species, the focus

of the current study was to model the potential maladaptation of Tasmanian populations to future climate change, without the option of translocating into Tasmania potentially less maladapted populations from the mainland. Therefore, species occurrence data for the 30 eucalypt species found in Tasmania were obtained from the Natural Values Atlas (http://www.naturalvaluesatlas.tas.gov.au/; accessed 6 February 2015), yielding 71,527 point occurrences. Duplicate occurrences and occurrences within 800 m of another were removed to limit the overrepresentation of a particular environment (Anderson and Gonzalez 2011). Spatial and environmental outlying occurrence records were identified using a modified *z*-score test following Jordan *et al.* (2016) and were manually checked against known distribution descriptions and removed where appropriate. This process yielded a final data set with 40,959 occurrence records (Table 2.1).

2.2.3 Environmental data

The distribution of suitable habitat for a species can be summarised as a function of light, temperature, water availability, nutrient availability, and topographic position (Luoto and Heikkinen 2008; Austin and Van Niel 2011). Twelve variables were used as proxies for each of these categories: light (solar radiation of the warmest quarter), temperature (minimum temperature of the coldest period, maximum temperature of the warmest period), water (precipitation of the wettest quarter, precipitation of the driest quarter), nutrient (percent total nitrogen, percent total phosphorous, plant exploitable depth, coarse fragments > 2 mm), and topographic position (slope, aspect). These variables were selected as they have been found to either limit the distribution margins of eucalypts in Tasmanian (Davidson and Reid 1985; Kirkpatrick and Gibson 1999), drive putative selection across the adaptive landscape (Austin and Van Niel 2011; Steane *et al.* 2014; Gauli *et al.* 2015; Harrison PA, Wilshire RJE, Potts BM (unpublished data)), or provide information on habitat heterogeneity across topographically complex landscapes (Luoto and Heikkinen 2008).

Table 2.1. The 30 eucalypt species of Tasmania, Australia. Species have been ordered by their taxonomic classification (subgenus and series within subgenera) (Brooker 2000). Species endemic to Tasmania are identified, along with their range size (Moran 1992) and their main occupied habitat type (Williams and Potts 1996). Also shown are the number of occurrence records (points) obtained from the Natural Values Atlas, the mean altitude, and the contemporary (1976-2005) mean annual temperature (TANN, ˚C) and mean annual precipitation (RANN, mm) range across each species distribution.

Species	Series	Endemic	Range size	Habitat	Distribution points	Altitude (m a.s.l)	TANN (°C)	RANN (mm)
Subgenus *Eucalyptus*								
E. amygdalina	*Aromatica*	E	Widespread	Dry sclerophyll	5826	199	8.3 - 13.4	546 - 1541
E. coccifera	*Aromatica*	E	Regional	Subalpine	644	990	5.2 - 9.9	716 - 2364
*E. nebulosa**	*Aromatica*	E	Rare	Wet sclerophyll	3	264	10.0 - 11.3	1952 - 2326
E. nitida	*Aromatica*	E	Widespread	Subalpine	1268	172	7.5 - 13.6	708 - 2685
E. pulchella	*Aromatica*	E	Regional	Dry sclerophyll	1098	210	9.0 - 12.8	550 - 1106
E. radiata	*Aromatica*		Rare	Dry sclerophyll	50	360	7.5 - 11.1	1344 - 2049
E. risdonii	*Aromatica*	E	Rare	Dry sclerophyll	84	138	11.1 - 12.5	531 - 634
E. tenuiramis	*Aromatica*	E	Regional	Dry sclerophyll	1009	235	9.1 - 13.1	533 - 1017
E. delegatensis	*Cineracea*	E	Widespread	Wet sclerophyll	4297	647	6.4 - 11.6	623 - 2051
E. pauciflora	*Cineracea*		Widespread	Subalpine	1069	495	6.6 - 13.3	493 - 1603
E. sieberi	*Cineracea*		Regional	Dry sclerophyll	608	183	9.9 - 13.4	655 - 1104
E. obliqua	*Eucalyptus*		Widespread	Wet sclerophyll	7788	234	8.8 - 12.9	631 - 1750
E. regnans	*Eucalyptus*		Widespread	Wet sclerophyll	2022	365	8.4 - 12.5	801 - 1590
Subgenus *Symphyomyrtus*								
E. barberi	*Foveolatae*	E	Regional	Dry sclerophyll	153	273	9.8 - 13.1	565 - 893
E. brookeriana	*Foveolatae*		Widespread	Wet sclerophyll	404	329	8.7 - 13.1	610 - 1860
E. ovata	*Foveolatae*		Widespread	Dry sclerophyll	2485	145	9.0 - 13.5	516 - 1365
E. rodwayi	*Foveolatae*	E	Widespread	Wet sclerophyll	577	617	6.9 - 12.8	502 - 1873
E. globulus	*Globulares*		Widespread	Wet sclerophyll	2865	154	9.4 - 13.6	551 1208

Continued from page 33

Species	Series	Endemic	Range size	Habitat	Distribution points	Altitude (m a.s.l)	TANN (°C)	RANN (mm)
E. archeri	*Orbiculares*	E	Regional	Subalpine	95	1137	4.8 - 8.7	874 - 1863
E. cordata	*Orbiculares*	E	Regional	Wet sclerophyll	86	308	8.8 - 12.3	618 - 1167
E. gunnii	*Orbiculares*	E	Regional	Subalpine	518	975	5.6 - 9.6	728 - 2196
*E. morrisbyi**	*Orbiculares*	E	Rare	Dry sclerophyll	5	30	12.0 - 12.7	558 - 587
E. urnigera	*Orbiculares*	E	Regional	Subalpine	130	789	5.7 - 10.8	715 - 1411
E. johnstonii	*Semiunicolores*	E	Regional	Subalpine	204	636	6.5 - 10.7	874 - 1849
E. subcrenulata	*Semiunicolores*	E	Regional	Subalpine	247	854	5.5 – 10.0	1030 - 2356
E. vernicosa	*Semiunicolores*	E	Regional	Subalpine	160	772	5.7 - 10.8	1150 - 3280
E. dalrympleana	*Viminales*		Widespread	Wet sclerophyll	1348	631	6.5 - 11.5	581 - 1693
*E. perriniana**	*Viminales*		Rare	Dry sclerophyll	7	566	9.0 - 9.8	668 - 871
E. rubida	*Viminales*		Regional	Dry sclerophyll	312	431	8.2 – 12.0	515 - 1037
E. viminalis	*Viminales*		Widespread	Dry sclerophyll	5597	223	8.4 - 13.3	526 - 1457

Light, temperature and water variables representing the contemporary and future climate were calculated under the Climate Futures for Tasmania project (Corney *et al.* 2010) at a spatial resolution of 30 seconds (*ca.* 0.8 km). Contemporary light, temperature and water surfaces were modelled using ANUCLIM version 6.1 (Xu and Hutchinson 2012) as the mean for the 30-year baseline period (1976-2005) centred on 1990. Future projections for the light, temperature, and water variables were obtained from dynamically downscaled models using six GCMs (ECHAM5/MPI-OM, CSIRO Mk 3.5, GFDL-CM2.0, UKMO HadCM 3, GFDL-CM2.1 and MIROC3.2 (medres); Table 2.2) for three future time periods that represented the 30-year average of 2010-2039, 2040–2069, and 2070–2099 (hereafter 2020s, 2050s, and 2080s) (see Corney *et al.* 2010 for further details). These GCMs were selected by Corney *et al.* (2010) as they provided good representations of the current range and variability in temperature and precipitation across south-eastern Australia, in addition to producing credible replication of the El Niño Southern Oscillation (Smith and Chandler 2010). Future projections were developed using the A2 emission scenario, which represents a high greenhouse gas emission scenario broadly similar to the newly described Representative Concentration Pathway (RCP) 8.5 (IPCC 2013). The A2 emissions scenario represents a conservative approach for modelling the distribution of a species as it assumes little global mitigation of greenhouse gas emissions, which is consistent with the current trajectories of global emissions (Peters *et al.* 2012), despite a recent plateau (Jackson *et al.* 2016).

Table 2.2. Details of the six global circulation models used in the current study, showing the current (1976-2005) mean annual temperature (TANN, ˚C) and mean annual precipitation (RANN, mm) for Tasmania, and the projected mean change in TANN and percent change in RANN by each global circulation model by the 2080s (2070-2099).

Global circulation model	Country	Reference	TANN (°C)	RANN (%)
		Current	10.5	1298.6
CSIRO Mk 3.5	Australia	Gordon *et al.* (2010)	2.9	0.7
ECHAM5/MPI-OM	Germany	Stevens *et al.* (2013)	2.2	1.6
GFDL-CM2.0	USA	Delworth *et al.* (2006)	2.2	3.0
GFDL-CM2.1	USA	Delworth *et al.* (2006)	2.3	1.7
MIROC3.2(medres)	Japan	Abe-ouchi (2004)	2.6	-0.1
UKMO HADCM3	United Kingdom	Johns *et al.* (2003)	2.7	13.3
		Grand mean	*2.5*	*3.4*

Soil layers were obtained from the compiled Tasmanian Soil Attribute Grids database (http://doi.org/10.4225/08/5472DCFDDFB67, accessed 2nd Oct 2016) and the Australian three-dimensional soil grids (Viscarra Rossel *et al.* 2015) at a resolution of 3 seconds. Soil attributes (percent total nitrogen, percent total phosphorous, soil coarse fragment) from multiple depth horizons were aggregated to give the mean value in a 2 m soil profile. Soil surfaces were then upscaled to 30 seconds to align with the spatial resolution of the light, temperature, and water surfaces using nearest-nighbour resampling by the *raster* package (Hijmans 2016) in R (R Core Team 2016). Although the upscaling of the soil surfaces smooths micro-site variation, these surfaces provided a broad-scale representation of interpolated edaphic conditions experienced by Tasmanian eucalypts.

Topographic features of the landscape can provide a buffer from climatic extremes and form drainage basins which can support species survival in marginal habitats. Ignoring topographic heterogeneity has been shown to result in biased predictions of suitable habitat with decrease model accuracy (Luoto and Heikkinen 2008). As climate data (see above) was adjusted for altitudinal variation, we included the topographic features of slope (degrees) and aspect (degrees) which were

calculated from a 9 second Australian bathymetric and topographic grid (Geoscience Australia; http://www.ga.gov.au) using eight neighbouring cells calculated by the 'terrain' function of the *raster* package. Slope and aspect layers were upscaled to align with the 30 second resolution of the other variables using nearest-neighbour resampling.

2.2.4 Modelling habitat suitability under climate change

The contemporary and future distribution of suitable habitat for the Tasmanian eucalypts was modelled using the Random Forest algorithm (Breiman 2001) implemented in the *randomForest* package (Liaw and Wiener 2002). Random Forest is a data driven, machine-learning algorithm which uses a bootstrapped subsample of the original data to create an ensemble of de-correlated classification trees. Random Forest was used as it is robust against over-fitting (Breiman 2001), can detect and handle complex non-linear relationships and interactions between predictor variables (Jones and Linder 2015; Wager and Walther 2015), and can handle moderate levels of collinearity among predictor variables (Dormann *et al.* 2013). We grew 1000 trees to classify the presence or absence of suitable habitat for each species using a balanced number of presences to pseudo-absences, where pseudo-absences were randomly sampled across the environmental space of Tasmania. Following Breiman (2001), the number of randomly selected predictor variables (*mtry*) used as candidates for splitting a node was optimised by fitting preliminary models with (i) $mtry = \sqrt{p} \times 0.5$, (ii) $mtry = \sqrt{p}$, and (iii) $mtry = \sqrt{p} \times 2$, where p is the number of predictor variables in the variable set X. The optimal *mtry* number was selected by minimising the out-of-bag (OOB) error while maximising the discrimination power of the model (Gini index). The OOB samples are the data points which do not contribute to the bootstrapped subsample, and the use of OOB samples is equivalent to a K-fold cross-validation which is performed as the forest is grown (Cutler *et al.* 2007; Hastie *et al.* 2009). The Gini index was calculated as Gini = $2 \times (AUC - 0.5)$, where AUC is the area under the receiver-operating curve (Engler *et al.* 2004), and ranged from 0 (model is

uninformative) to 1 (model perfectly discriminates). The Gini index (as well as other evaluation statistics – Appendix A2) was estimated for each species using a confusion matrix that was derived from a test data set (withheld 30% random sample of the data) that did not contribute to the training of the Random Forest model. The importance of each predictor variable in the final, optimised model was also estimated using the percent increase in predictive error by randomly permuting the OOB samples for a variable while holding all other predictor variables unchanged (Liaw and Wiener 2002). Preliminary models for three species (*Eucalyptus morrisbyi*, *E. nebulosa*, *E. perriniana*) were found to be uninformative, most likely due to the rarity of these species (< 7 occurrences, Table 2.1), and were removed from further analyses.

The optimised model was predicted onto the contemporary and future environmental surfaces (see above) to produce a spatial binary layer of habitat suitability using the *raster* package. Predictions of suitable habitat under the six GCMs were summed for each species to produce a species-level habitat suitability layer. The habitat suitability layers were further refined by removing grid cells where equal to or less than two GCMs were in consensus. Models were spatially evaluated by first estimating the percent of occurrence records correctly classified, then by quantifying the over-prediction of the model by comparing the area of predicted suitable habitat to the area currently occupied by each species within a convex α-hull calculated using an $\alpha = 0.1$ and the 'ahull' function of *alphahull* (Pateiro-Lopez and Rodriguez-Casal 2016).

2.2.5 Quantifying changes in species diversity

To quantify the spatiotemporal shift in species diversity due to climate change we calculated the local (alpha) diversity of eucalypts using species richness which was calculated as the number of species within a 1 km grid cell. Contemporary species diversity was calculated using all occurrence records (see above). Future predictions of species diversity were calculated using only those occurrence records that were predicted to be within suitable habitat according to the Random Forest

models. Statistical significance of the spatiotemporal shift in species diversity was tested using the 'SigDiff' function of the *SDMTools* package (VanDerWal *et al.* 2014). This function computes the pixel pairwise differences between two prediction layers of suitable habitat, standardised to a unit variance, and tests the pixel-wise significance using a z-score test.

2.2.6 Direction of spatial shift in suitable habitat

The contemporary and future centroid of suitable habitat for each of the 27 eucalypt species was calculated using the 'COGravity' function of the *SDMTools* package. This function used a weighted mean and standard deviation between the contemporary and 2080s prediction of suitable habitat to determine the direction and magnitude of projected range shifts for a species.

2.2.7 Predicting the susceptibility of populations to climate change

To test whether a species characteristics predicted increased risk of maladaptation to climate change, we calculated two metrics derived from the predictions of the Random Forest model. The first metric assessed changes in the contemporary ($AREA_C$) and future ($AREA_F$) area of suitable habitat as: $SH_{AREA} = ((AREA_F – AREA_C) / AREA_C)$ (Zhang *et al.* 2015). The second metric assessed changes in the number of contemporary ($POINTS_C$) and future ($POINTS_F$) occurrences in suitable habitat as: $OR_{POINTS} = 100 - ((POINTS_F / POINTS_C) * 100)$, which conceptually follows the approach outlined by Booth (2017a). A non-parametric Kruskal-Wallis rank sum test was used to determine whether the group-wise mean of the two response metrics statistically differed among taxonomic groups (subgenera and series within subgenus; classification follows Brooker 2000), endemic *versus* non-endemic, range extents (widespread, regional, rare; Moran 1992), and habitat types (wet/dry sclerophyll, subalpine; Williams and Potts 1996). When statistically significant differences were detected, a Dunn's test of multiple comparisons using ranked sum was conducted, with significance adjusted for false discoveries using the Benjamini-Yekutieli False Discovery Rate adjustment (Benjamini and Yekutieli 2001). As *E. globulus* is the only representative of the series

Globulares (Brooker 2000), it was excluded from the test among taxonomic lineages. The relationship between SH_{AREA} and OR_{POINTS} was assessed using a simple linear regression model. To meet normality and homoscedasticity of variance assumptions, SH_{AREA} was $\log_{10}$ transformed for the statistic test, then back-transformed to visualise the relationship.

2.2.8 Evaluating the effectiveness of current reserve systems

Tasmania has over 30,000 formal and informal reserves that are protected under various levels of Commonwealth and State legislation. While an assessment of all 30,000 reserves is outside the scope of the current study, we focused on reserves that were ≥ 10 ha in area which was judged to represent a minimum size for maintaining the evolutionary potential of a eucalypt population (see below). This resulted in 5,918 reserves obtained from the Tasmanian LISTmap (http://maps.thelist.tas.gov.au/listmap/app/list/map; accessed 5th Jan 2017; Appendix A1) that range in area from 10 ha to 605,667 ha, and these represent in total 22% of the protected area. To quantify the 'effectiveness' of the reserve estate in protecting the Tasmanian eucalypts, we used two dispersal scenarios that reflect the likely seed-mediated gene flow by eucalypts across the landscape. Eucalypt seed has limited dispersal capabilities when shed (Cremer 1977; Booth 2017b) and to reflect this the first scenario was to allow 'no dispersal'. This scenario prevents a species colonising a neighbouring grid cell with newly available suitable habitat. The 'no dispersal' scenario is similar to Hamann and Aitken's (2013) 'adaptation only' scenario and reflects the three trajectories a population may follow; persistence, adaptation, or extirpation. To account for potential rare long-distance seed dispersal (Ashton 2000), we used a second scenario that allowed 'limited dispersal'. Under this scenario, a species was able to disperse into a grid cell with suitable habitat if that grid cell was within 10 km of an occurrence record.

The two dispersal scenarios were used to assess whether the current reserve systems in Tasmania maintained sufficient habitat for species under projected climate change. We first summed the

number of occurrence points *d* within each reserve *r* relative to all occurrence points of a species *D* through time:

$$ppt = \sum_{r=1}^{R} \frac{\{d \in r\}}{D}$$

The 'effectiveness' of reserve *r* was quantified as the product of the predicted area by the Random Forest model and the proportion of distribution points *ppt* within the reserve. Following Hamman and Aitken (2013), the total number of effective reserves was quantified as the sum of reserves with ≥ 10 ha of suitable habitat during any given time period. While species, age and habitat dependent, the 10 ha minimum used here would correspond to approximately 160 stems/ha in a woodland (Prober and Brown 1994; Gibbons *et al.* 2010) or 400 stems/ha in an early- to mid-aged (40 years old) continuous forest (Ashton 1976).

2.3 Results

2.3.1 Evaluation of the Random Forest models

The generally low out-of-bag error (0.07 – 0.30) and moderate Gini Index (0.41 – 0.58) (Appendix A2) suggests the Random Forest models were capable of differentiating the true occurrences from pseudo-absences. The moderate Gini Index scores likely reflect the random sampling of the pseudo-absences, where some pseudo-absences occurred within suitable habitat. Nevertheless, the models were sensitive enough to detect occurrences that were potentially misclassified, such as occurrences along the margins between the distributions of *Eucalyptus amygdalina* and *E. nitida* which represent intergrading populations (Appendix A3; Williams and Potts 1996). Spatial prediction of the models showed there was a tendency to over-predict the contemporary suitable habitat when compared to the area of the convex α-hull of occurrences (Appendix A3). However, this was not the case for widespread species which tended to slightly

under-predict area of suitable habitat (Appendix A3). Nevertheless, overall the models were able to capture on average 95% of species occurrences.

2.3.2 Temperature and precipitation most important predictor variables

Maximum summer temperatures, minimum winter temperatures, and the amount of winter precipitation were the most important variables when modelling the contemporary distribution of the Tasmanian eucalypts. Summer radiation was an influential variable for species from the *Aromatica* lineage (the informal peppermint group, Williams and Potts 1996), but was generally not as important for the other species (Appendix A4). Edaphic factors showed intermediate importance in the models, with the percent of coarse fragments > 2 mm in a 2 m soil profile being consistently the most important edaphic variable (Appendix A4). Surprisingly, topographic variables contributed little to the models (Appendix A4).

2.3.4 Future climates increase the vulnerability of species to maladaptation

The change in suitable habitat under future climates was progressive through time, with the greatest change occurring between the 2050s and 2080s (Appendix A5). The models predict that 25 of the 27 eucalypt species will lose on average 60% of contemporary suitable habitat by the 2080s (Table 2.3; Appendix A5). This is predicted to have a considerable impact on globally important species (i.e. the world's tallest angiosperm *E. regnans*), species that are important habitat for endangered species (i.e. *E. globulus* which is critical for the endangered swift parrot, *Lathamus discolour*; Saunders and Tzaros 2011), and key species for ecological restoration in Tasmania (i.e. *E. pauciflora* and *E. ovata*) (Figure 2.2). Only *E. radiata* and *E. risdonii* were expected to gain more suitable habitat by the 2080s (Table 2.3; Appendix A5). This finding is not surprising, especially for the dry adapted *E. risdonii* which is predicted to gain considerable habitat in the Midlands of Tasmania by the 2080s (Figure 2.2), a region which currently has the most arid environment on the island.

Table 2.3. Summary of the predicted changes in the distribution of modelled suitable habitat for 27 Tasmanian eucalypt species by the end of this century. Shown are the predicted range shifts (km) and altitude deplacement (m above sea level) in the suitable habitat centroid between the contemporary (1976-2005) and 2080s models based on a centre of gravity (COG) shift, the percent change in area predicted by the models of contemporary and 2080s suitable habitat, and the percentage of observed occurrences predicted to be outside suitable habitat modelled under contemporary (1976-2005) and 2080s climate and are likely to be at a higher risk of maladaptation . Positive COG shifts in altitude indicate a upslope displacement of the modelled suiatable habitat.

Species	COG shift by 2080s (km)	Δ COG shift in altiude by 2080s (m a.s.l)	% change in future suitable climate (2080s)	Occurrences outside suitable habitat (%)	
				Current	2080s
Subgenus *Eucalyptus*					
Eucalyptus amygdalina	31	277	-13	7	55
Eucalyptus coccifera	14	7	-90	4	83
Eucalyptus nitida	53	-355	-70	12	89
Eucalyptus pulchella	23	129	-47	11	73
Eucalyptus radiata	21	-332	50	4	18
Eucalyptus risdonii	30	1	157	1	5
Eucalyptus tenuiramis	23	166	-66	13	84
Eucalyptus delegatensis	26	64	-70	2	80
Eucalyptus pauciflora	26	82	-82	3	83
Eucalyptus sieberi	23	-174	-59	4	81
Eucalyptus obliqua	32	-327	-51	6	77
Eucalyptus regnans	30	-507	-50	2	64
Subgenus *Symphyomyrtus*					
Eucalyptus barberi	23	-127	-23	0	23
Eucalyptus brookeriana	52	-348	-38	4	72
Eucalyptus ovata	6	33	-2	9	23
Eucalyptus rodwayi	30	-57	-73	3	78
Eucalyptus globulus	29	138	-62	16	80
Eucalyptus archeri	24	182	-93	1	78
Eucalyptus cordata	7	-61	-52	7	49
Eucalyptus gunnii	15	259	-88	5	95
Eucalyptus urnigera	9	311	-62	5	38
Eucalyptus johnstonii	12	466	-75	1	54
Eucalyptus subcrenulata	15	186	-80	4	74
Eucalyptus vernicosa	28	267	-88	6	54
Eucalyptus dalrympleana	37	541	-73	2	84
Eucalyptus rubida	21	457	-67	0	62
Eucalyptus viminalis	28	343	-25	8	57
Mean					
All species	*24.8*	*60.8*	*-47.8*	*5.2*	*63.4*
Endemics only	*27.5*	*108.4*	*-39.1*	*5.2*	*63.8*

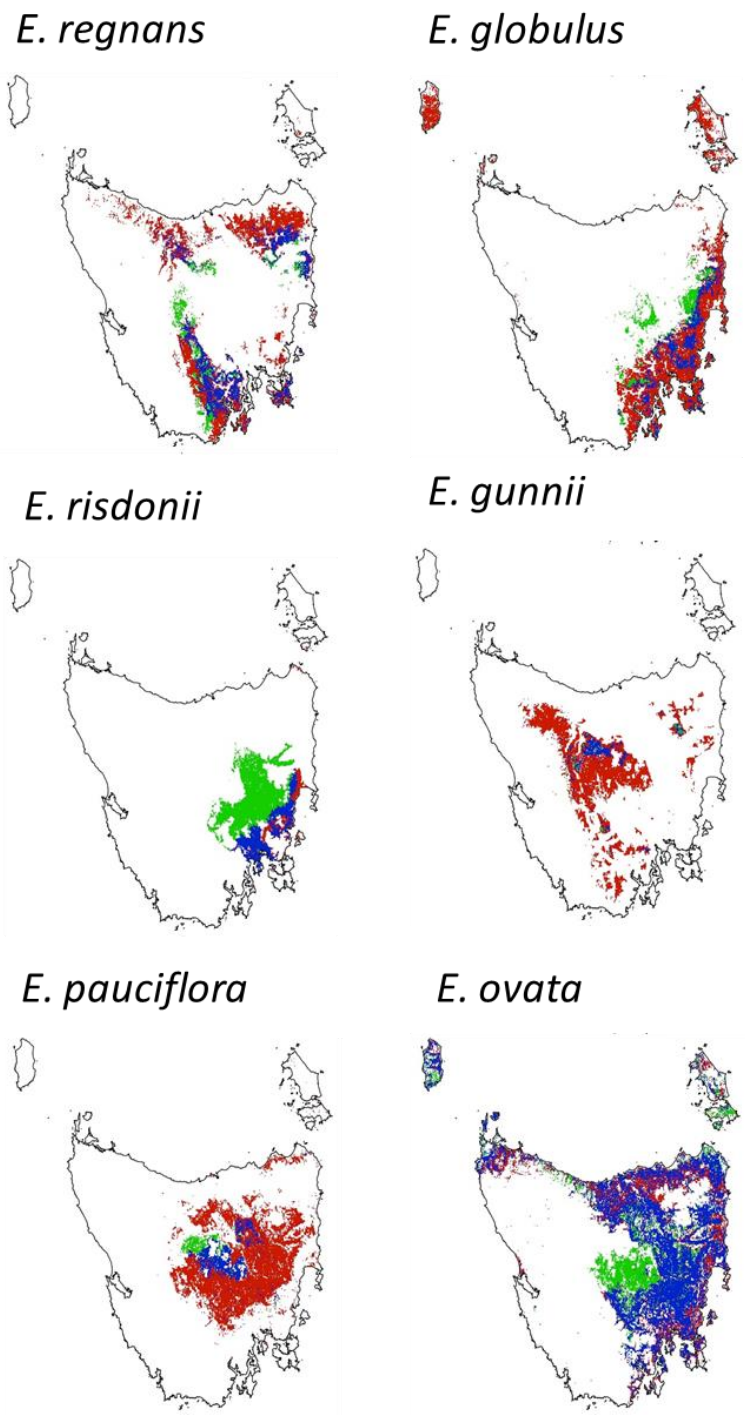


Figure 2.2. The extent of modelled suitable habitat by the end of this century (2080s [2070-2099]) that is predicted to be outside (red) or within (blue) current suitable habitat range, or become suitable habitat (green). The selected examples represent species that are globally important (*E. regnans*, *E. globulus*), endemic (*E. risdonii*, *E. gunnii*), or locally important for ecological restoration (*E. pauciflora*, *E. ovata*). See Appendix A5 for the other 21 species.

The direction and magnitude of the suitable habitat centroid varied among species, with an average shift of 25 km by the 2080s (6 km to 53 km; Table 2.3) which corresponded to an average displacement of 0.26 km per year (0.06 km to 0.56 km per year). There was a general westward shift in the centroid of most species, with the habitat of some species showing an upslope shift onto the Central Plateau by the 2080s (Table 2.3; Figure 2.3). Indeed, there was a general upslope displacement of the centroid of the species modelled suitable habitat. This upslope displacement averaged 61 m, with endemic species showing the greatest average displacement (Table 2.3). As the centroid moved across the landscape, there was an overall significant negative relationship between the area of current suitable habitat lost and the vulnerability of occurrences to maladaptation (R^2 = 0.82, $F_{1, 25}$ = 112.0, P < 0.001; Figure 2.4). Some species, however, were more impacted by shifts in their centroid of suitable habitat. For example, the centroid of suitable habitat for *E. amygdalina* was predicted to move 31 km by the 2080s resulting in a loss of 13% of its current suitable habitat. This, however, was predicted to lead to 55% of its occurrences to be maladapted (outside predicted suitable climate habitat) under 2080s climate (Table 2.3). Furthermore, a slight 6 km shift in the centroid of suitable habitat for *E. ovata* by the 2080s resulted in a 2% reduction in currently suitable habitat, yet 23% of its occurrences are predicted to be maladapted to 2080s climates (Table 2.3). These examples suggest that the loss of suitable habitat may not always reflect the extent of maladaptation risk for current occurrences of a species.

2.3.5 Non-uniform change in species diversity

Under current climate conditions, the north-east coast and the south-east of Tasmania had the highest levels of observed species diversity (Figure 2.5). While still having patches of high diversity, the centre and north-west of Tasmania generally had the lowest species richness (Figure 2.5). Under future climates, regions that currently maintain high diversity tended to remain centres of species diversity. However, significant decreases in species richness (based on occurrences with future suitable habitat) were detected (Appendix A6).

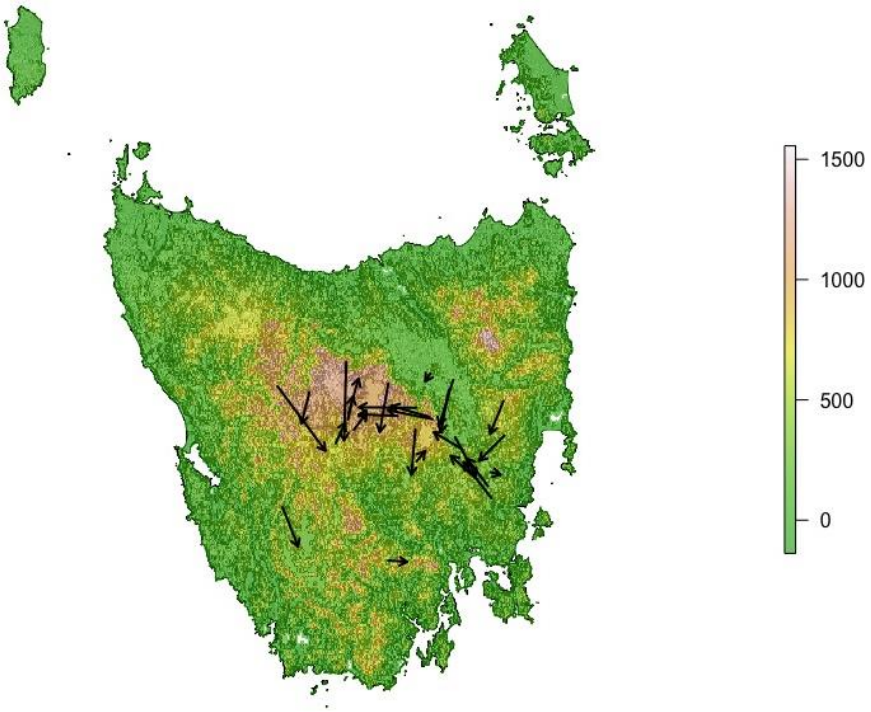


Figure 2.3. The predicted spatial shift in the mean centre of gravity (COG) of suitable habitat between the contemporary (1976-2005) and 2080s models. The length of the arrow corresponds to the predicted magnitude shift, and the arrow head represents the centroid by the 2080s while the arrow base is the current position. Also shown is the elevation map over a hillshade (see Figure 2.1 for more detail).

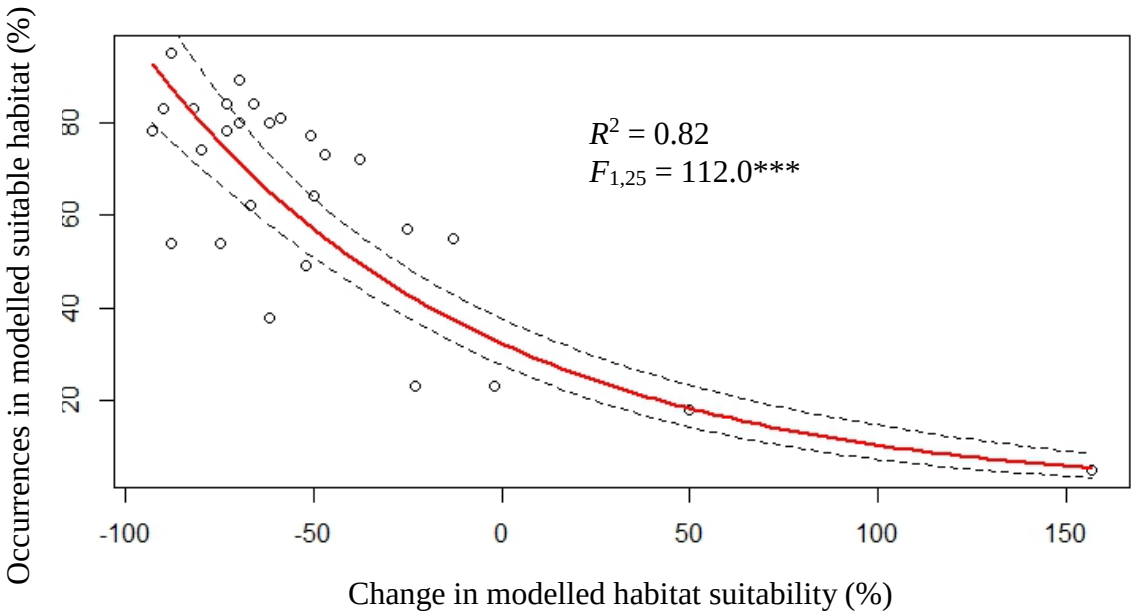


Figure 2.4. The negative decay relationship between the percent change in habitat suitability and the percent change in occurrences within modelled suitable habitat by the 2080s for each of the 27 eucalypt species. Species are represented by open circles and the red line shows the fit of the linear model through these points along with the 95% confidence intervals (black dashed lines).

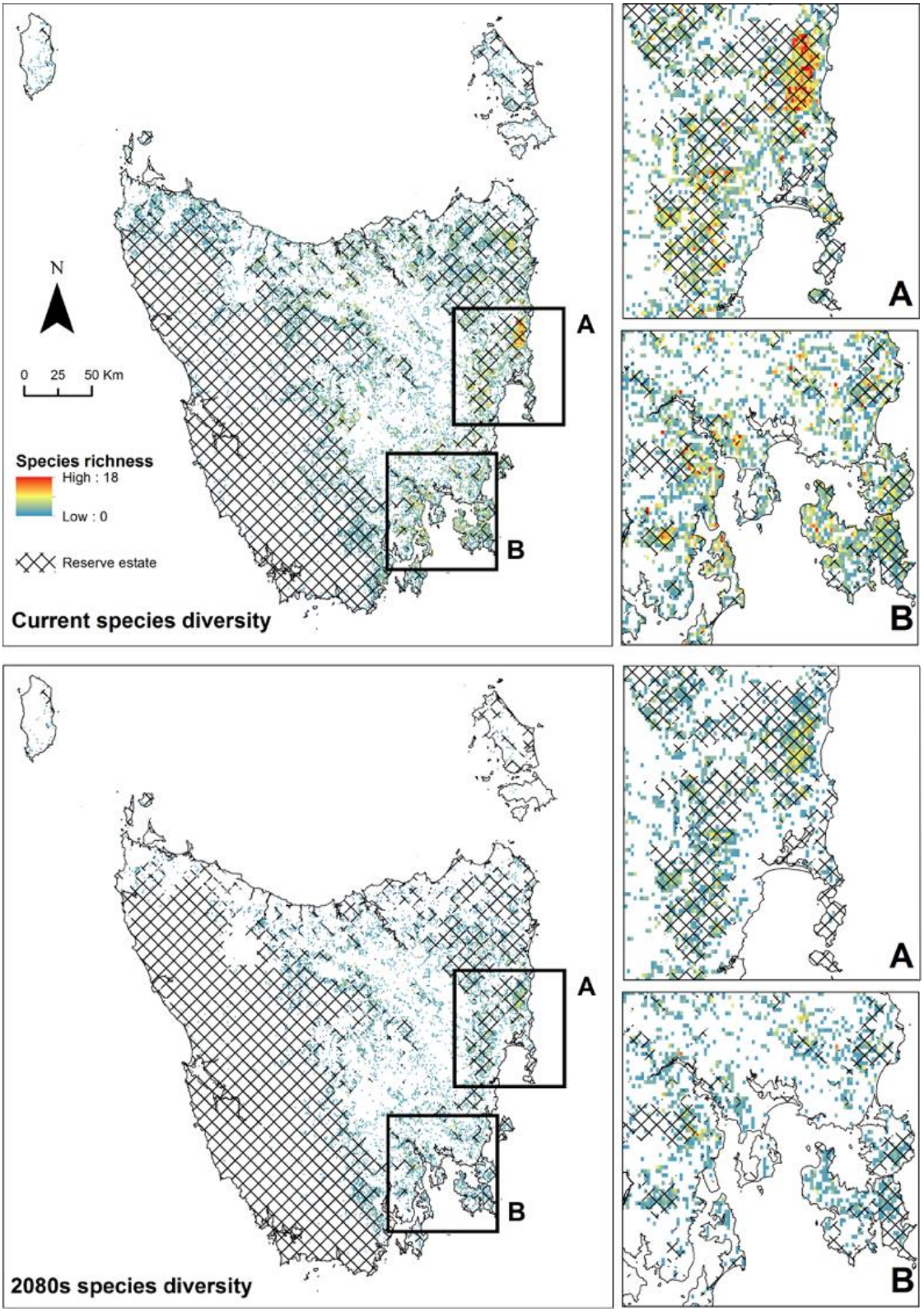


Figure 2.5. Contemporary (1976-2005) and future (2080s) species diversity for the Tasmanian eucalypts. Inset maps A and B highlight two current hotspots of eucalypt diversity. Species richness was calculated using the occurrence records occupying modelled suitable habitat, assuming a 'no dispersal' scenario. Species diversity has been scaled to between 0 (cool colours) to 18 (warm colours) based on current observed diversity. The hatching represents the current Tasmanian reserve estate.

2.3.6 What predicts species risk of maladaptation under climate change?

Although species of subgenus *Symphyomyrtus* showed a greater decline in future suitable habitat compared to subgenus *Eucalyptus* (Figure 2.6), there was no significant difference between subgenera for the area of suitable habitat (SH_{AREA}; χ_1^2 = 1.26, $P > 0.05$) or occurrences within the modelled suitable habitat (OR_{POINTS}; χ_1^2 = 1.15, $P > 0.05$). The taxonomic groups varied in their percentage of lost current suitable habitat and risk of maladaptation (i.e. occurrences outside modelled habitat) under future climates, with species from *Semiunicolores* being most at risk (Figure 2.6). However, there was no significant differences among the taxonomic groups (SH_{AREA}: χ_6^2 = 9.26, $P > 0.05$; OR_{POINTS}: χ_6^2 = 4.24, $P > 0.05$) nor between endemics and non-endemics (SH_{AREA}: χ_1^2 = 2.65, $P > 0.05$; OR_{POINTS}: χ_1^2 = 0.00, $P > 0.05$). We did detect significant differences among the range size of species (SH_{AREA}: χ_2^2 = 7.80, $P < 0.05$; OR_{POINTS}: χ_2^2 = 5.86, $P < 0.05$), with the rare species (*E. radiata* and *E. risdonii*) gaining significantly more modelled suitable habitat and having few occurrences at risk of maladaptation under future climates compared to widespread and regional species (Figure 2.6). Species from subalpine habitats showed significantly higher reduction in modelled current suitable habitat under future climates (SH_{AREA}: χ_2^2 = 17.07, $P < 0.001$), however, this did not correspond to a significant difference in occurrences at risk of maladaptation under future climates predicted for these habitat types (OR_{POINTS}: χ_1^2 = 4.26, $P > 0.05$), despite the high percentage of occurrences at risk of maladaptation by the 2080s (Figure 2.6).

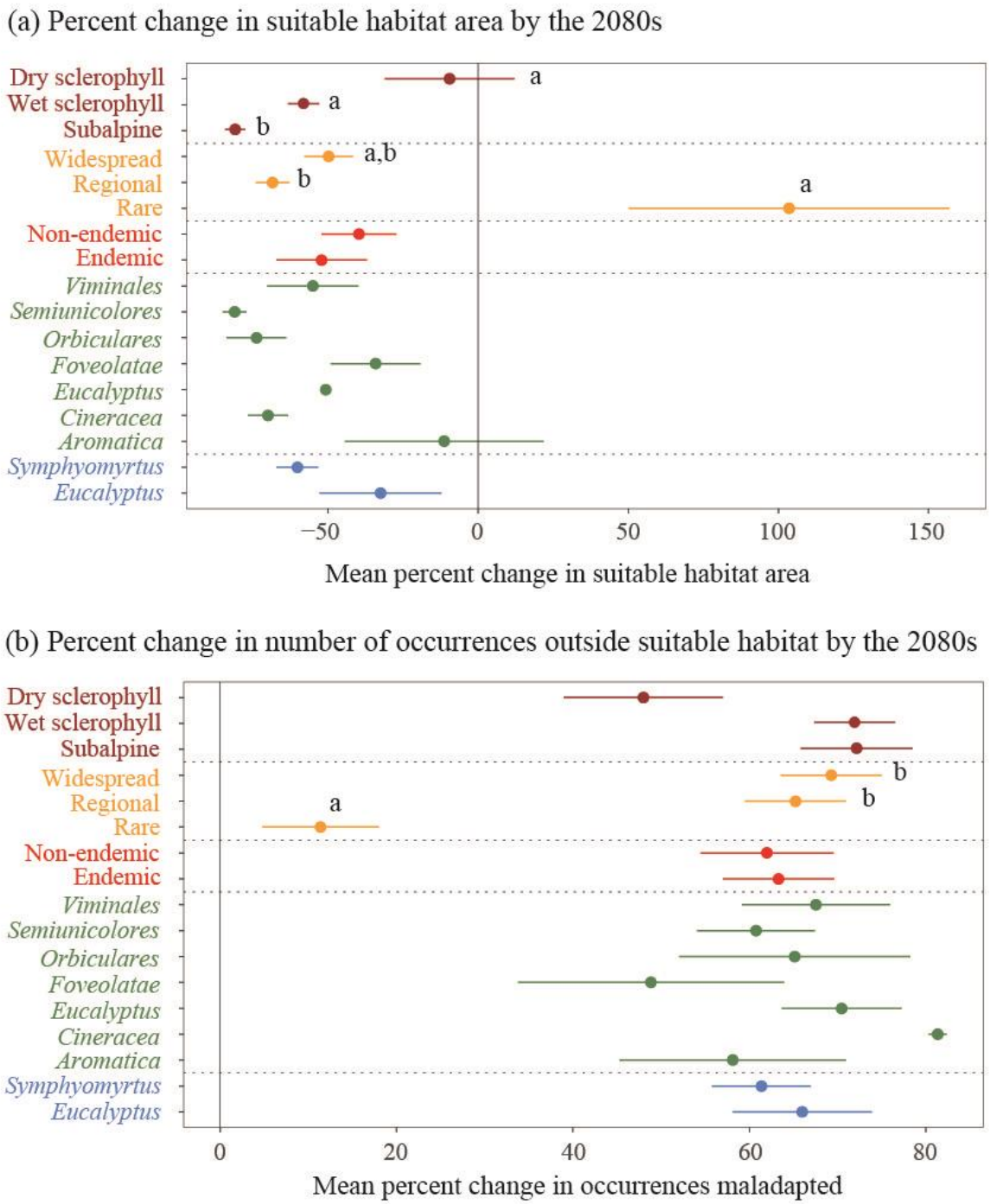


Figure 2.6. Mean (filled circles) and standard errors (bars) for the change in (a) suitable habitat area by the 2080s (SH_{AREA}) and (b) number of occurrence records not within suitable habitat (OR_{POINTS}). Statistically significant changes in SH_{AREA} and OR_{POINTS} among group means within habitat type (brown), range extent (yellow), endemism (red), series within subgenera (green) (Brooker 2000), and subgenera (blue) were tested using a Kruskal-Wallis tests, where letters denote significant ($P < 0.05$) differences among groups after a Benjamini-Yekutieli False Discovery Rate adjustment.

2.3.7 Assessment of current reserve systems under future climates

Eucalypts have a varied level of protection within the current reserve estate of Tasmania, with reserves containing on average 46% of a species occurrences (Table 2.4). *Eucalyptus rubida* had the lowest proportion (0.09) of occurrences in current reserves, while *E. subcrenulata* and *E. vernicosa* were the most protected (1.00; Table 2.4). The reserve estate effectively maintained contemporary suitable habitat for all species, especially those species confined to western Tasmania or high altitude sites (Table 2.4). Under future climates and assuming a 'no dispersal' scenario, the number of effective reserves that maintain at least 10 ha will be greatly reduced from a mean of 28% under current climates to 8% by the 2080s, with species from subgenera *Eucalyptus* on average least effectively reserved by the 2080s (Table 2.4). However, by allowing for limited migration into these reserves, the number of reserves that will effectively maintain adequate habitat increased nearly two-fold (relative to the 'no dispersal' scenario) by the 2080s (Table 2.4).

Table 2.4. Proportion of occurrence records within current and 2080s suitable habitat contained within reserves and the number of effective reserves that maintain sufficient suitable habitat (modelled area * species proportion > 10 ha) under a 'limited dispersal' and 'no dispersal' scenario.

Species	Proportion in reserve		Limited dispersal		No dispersal	
	Current	2080	Current	2080s	Current	2080s
Subgenus *Eucalyptus*						
Eucalyptus amygdalina	0.30	0.13	71	36	47	16
Eucalyptus coccifera	0.69	0.14	57	15	32	11
Eucalyptus nitida	0.47	0.09	99	14	43	6
Eucalyptus pulchella	0.23	0.12	32	18	16	11
Eucalyptus radiata	0.90	0.94	15	13	12	10
Eucalyptus risdonii	0.25	0.25	2	2	2	2
Eucalyptus tenuiramis	0.23	0.03	27	5	18	0
Eucalyptus delegatensis	0.60	0.14	105	33	81	21
Eucalyptus pauciflora	0.16	0.01	30	2	13	0
Eucalyptus sieberi	0.77	0.17	48	12	43	10
Eucalyptus obliqua	0.37	0.12	92	26	71	11
Eucalyptus regnans	0.55	0.23	92	40	68	23
Subgenus *Symphyomyrtus*						
Eucalyptus barberi	0.39	0.35	33	26	23	19
Eucalyptus brookeriana	0.50	0.12	57	24	17	8
Eucalyptus ovata	0.12	0.08	29	21	10	8
Eucalyptus rodwayi	0.21	0.03	43	7	14	0
Eucalyptus globulus	0.23	0.08	38	15	24	6
Eucalyptus archeri	0.63	0.12	38	6	24	6
Eucalyptus cordata	0.37	0.16	22	11	8	4
Eucalyptus gunnii	0.37	0.04	63	10	28	1
Eucalyptus urnigera	0.54	0.16	40	29	13	12
Eucalyptus johnstonii	0.79	0.28	52	20	22	9
Eucalyptus subcrenulata	1.00	0.36	49	13	19	6
Eucalyptus vernicosa	1.00	0.66	33	11	18	8
Eucalyptus dalrympleana	0.46	0.07	71	17	48	5
Eucalyptus rubida	0.09	0.05	28	7	7	2
Eucalyptus viminalis	0.26	0.14	60	27	41	12
Mean						
Overall	0.46	0.19	49	17	28	8
Subgenus *Eucalyptus*	0.46	0.20	56	18	37	10
Subgenus *Symphyomyrtus*	0.46	0.18	44	16	21	7

2.4 Discussion

Our results clearly show that large components of the eucalypt flora in Tasmania will be outside their current modelled climate range by the end of this century. This result agrees with a vast number of global (Thuiller *et al.* 2011; Lenoir and Svenning 2015; Zhang *et al.* 2015) and local (Butt *et al.* 2013; González-Orozco *et al.* 2016; Mokany *et al.* 2016) studies demonstrating the negative effects

of climate change on plant distributions. In Australia, eucalypts are expected to show a pole-ward displacement of their modelled suitable habitat (Butt *et al.* 2013; González-Orozco *et al.* 2016) consistent with Northern Hemisphere plant species (McKenney *et al.* 2007; Chen *et al.* 2011; Zhang *et al.* 2015). However, in Tasmania, the displacement of suitable habitat for eucalypts was predominantly in a westward direction towards mountainous regions. This is not a surprising result given the topographic complexity of the Tasmanian landscape. Temperatures in Tasmania decrease on average by 0.6°C for every 100 m gain in elevation (Jackson 2005), and this upslope response no doubt represents an 'altitude-for-latitude' displacement (Jump *et al.* 2009).

The extent to which the eucalypt flora will remain in current suitable habitat has a certain level of predictability. As expected, eucalypt species that occupy high altitude habitats were found to be more impacted under future climates than species that occupy dry and wet sclerophyll forests. High altitude plant species are likely to be among some of the most sensitive to future climate change (Dullinger *et al.* 2012). Indeed, even slight changes in annual temperature in these high altitude environments have triggered large-scale upslope migrations and changes in the composition of species communities across Europe (Grabherr *et al.* 1994; Gottfried *et al.* 2012). Although many species from the series *Orbiculares* and *Semiunicolores* frequently occupy the high altitude tree line in Tasmania (Williams and Potts 1996), we failed to detect a significant evolutionary signal (phylogenetic and endemicity) to climate change susceptibility. Previous studies have shown a link between phylogenies and the susceptibility of species to future climate change, with older lineages more susceptible than recently evolved lineages (i.e. neo-endemics) (Zhang *et al.* 2015; González-Orozco *et al.* 2016). But despite the deep evolutionary history of eucalypts on the island (McKinnon *et al.* 2004) and the potentially high frequency of neo-endemic species in the series *Aromatica* (i.e. *E. risdonii*, Potts and Wiltshire 1995), our results suggest that related species will not respond similarly to climate change. This is a positive result in the sense that eucalypt phylogenetic diversity in Tasmania is not expected to be greatly affected by climate change.

The extent to which eucalypt species are actually at risk of maladaptation as predicted by these models (i.e. outside modelled suitable habitat) is dependent on many factors, one of which is the width of their fundamental niche. The fundamental niche, as postulated by Hutchinson (1957), is the *n*-dimensional hyper-space comprising the biotic and abiotic components of the environment that permits a species to survive and reproduce indefinitely. The realised niche is therefore a discrete hyper-volume of the fundamental niche in which a species is competitive over all other species (Hutchinson 1957). By their definition, occurrence-only habitat suitability models at best represent the realised niche (Booth *et al.* 1988; Austin 2002) and are thus often over-pessimistic in their predictions. Indeed, species transplanted outside their natural range have shown the fundamental niche may be much wider than their realised niche (Booth *et al.* 1988; Booth 2015; Bocsi *et al.* 2016). However, as the environment continues to shift under future climate change, species will be pushed towards the suboptimal conditions on the boundary of their fundamental niche (Hutchinson 1957).

It is challenging to predict the ability of a species to persist (and for how long), but it is likely to be dependent on the level of adaptive genetic diversity maintained within populations (Jump *et al.* 2009) and the ability of the species to change their phenotype (i.e. adaptive and non-adaptive plasticity; Lande 2009; Chevin *et al.* 2010). Nevertheless, severe drought events attributed to recent climate change have seen rapid, large-scale forest dieback (Evans *et al.* 2013; Matusick *et al.* 2013; but see reviews by Jump *et al.* 2009 and Allen *et al.* 2010), indicating some species may already be at their ecological tipping points. The long-term persistence of a species under future climate change seems dependent on its ability to adaptively respond to on-going changes in two components of their niche; the ‘survival niche’ and the ‘regeneration niche’ (Grubb 1977; Bykova *et al.* 2012), discussed below.

Plants have numerous strategies that allow them to persist for a time in unsuitable habitats. Most of these strategies involve non-genetic phenotypic change (morphological and physiological) in response to a new selective pressures (Nicotra *et al.* 2010). Eucalypts have well-developed mechanisms for vegetative recovery following fire and other stresses (drought and herbivory) (Pryor 1976), which would likely enhance the persistence of pre-established individuals. Noteworthy features include the capacity of individuals to change habit (e.g. shift from a tree to a multi-stemmed mallee - Hopkins and Robinson 1981) and revert to an early life history form (Wiltshire *et al.* 1991). Adjustments can also occur at the stand-level by reductions in densities, which in water limited environments, may reduce the exposure of surviving individuals to water stress (White *et al.* 2009). As large components of modelled suitable habitat for the eucalypts in Tasmania redistributes across the landscape under future climates, it is therefore likely those occurrences found outside their modelled suitable habitat will persist through such strategies for a time, increasing opportunities for genetic adaptation to the new selective regimes. The ability for species to persist in their survival niche (also known as the 'tolerance niche' - Sax *et al.* 2013) nevertheless conceptually implies a much wider hyper-volume than their fundamental niche (Sax *et al.* 2013).

The regeneration niche is rarely considered when modelling species responses under future climate change (Bykova *et al.* 2012; Dormann *et al.* 2012), and it is a critical component that requires discussion in light of our results. The regeneration niche can be conceptualised as the combination of the 'reproduction niche' (the hyper-volume within the realised niche that promotes reproduction, such as initiation of flower formation), and the 'establishment niche' (the hyper-volume within the reproduction niche that promotes seed germination and seedling establishment – *sensu* Bailey *et al.* 2012). One of the first signals of maladaptation under climate change will likely manifest in the species regeneration niche. Already there are examples of various species with altered flowering patterns (Fitter and Fitter 2002; Calinger *et al.* 2013; CaraDonna *et al.* 2014) and

regeneration potential (Mok *et al.* 2012; Bell *et al.* 2014; Rawal *et al.* 2014; Keith and Myerscough 2016) under climate change. While plasticity in these traits can assist rapid adaptive evolution in just a few generations (Franks *et al.* 2007), there will certainly be ecological limits to phenotypic plasticity, especially for long-lived species with long generation times (Parmesan 2006; Valladares *et al.* 2007) such as eucalypts. Indeed, the on-going decline in health and reduced flowering of mature trees (Potts *et al.* 2001; Calder and Kirkpatrick 2008) coupled with the climate-induced redistribution of the establishment niche (Sanger *et al.* 2011) has led to the rapid decline in recruitment and extensive dieback of the high altitude *Eucalyptus gunnii*. The future predictions for *E. gunnii* indicate continued reduction in modelled suitable habitat, and points to the implications of how early maladaptation of the regeneration niche under current and future climate change may lead vulnerable species into an extinction vortex.

Whether a species can escape an extinction vortex under climate change will depend on its ability to disperse. The current study found that on average eucalypts in Tasmania will need to disperse 0.26 km per year to keep within modelled suitable habitat. This rate of dispersal is comparable with other modelled studies on eucalypts (González-Orozco *et al.* 2016), but is a much slower dispersal rate than those predicted for Northern Hemisphere plants (McKenney *et al.* 2007; Chen *et al.* 2011; Zhang *et al.* 2015). This may represent a disparity between the velocity and intensity of climate change between Northern and Southern Hemispheres. However, in the present case, the slower rate of dispersal may be partly explained by the steep environmental gradients which exist over short geographic distances due the rugged topography of Tasmania (Reid and Potts 2000). Nevertheless, even for plants such as eucalypts where seed-mediated dispersal is usually limited and recruitment periodic and dependent on disturbances such as fire (Ashton 2000; Nicolle 2006), the predicted rates may be difficult to achieve. Indeed, despite a 20-fold difference in seed output between *E. risdonii* and *E. amygdalina*, recruitment of *E. risdonii* following wildfire only resulted in

a 7 m expansion of its western boundary into the range of *E. amygdalina* (Potts 1986). Eucalypt seed generally lack specialised dispersal adaptations, and the canopy stored seed is mainly gravity dispersed within two canopy heights of the maternal tree (Cremer 1977; Barbour *et al.* 2005). Prevailing winds (Potts and Wiltshire 1995; Jones *et al.* 2007) and downslope water flow (Kirkpatrick 1977; Larcombe *et al.* 2013) are likely to impose strong directional asymmetry to seed-mediated migration (Kirkpatrick 1977; Munoz *et al.* 2004; Cook and Crisp 2005), creating a further challenge for upslope and westward migration from the lowland centres of diversity on the island.

Pollen-mediated dispersal, on the other hand, occurs through active and often wide ranging animal vectors (insects, birds, mammals), and pollen dispersal distances can far exceed that of seed dispersal (Barbour *et al.* 2005). While most pollen is distributed within a 200 m radius of the paternal tree, dispersal up to 1.6 km have been recorded (Barbour *et al.* 2005; Byrne 2008; Larcombe *et al.* 2016), and even greater distances have been suggested for migratory birds and mammal pollinators (Southerton *et al.* 2004). The often 'fat-tailed' pollen dispersal curves are likely to be important in the redistribution of genetic diversity within species, enhancing the possibility of local adaptation to climate change (Aguilée *et al.* 2016), especially when long-distance gene flow is from pre-adapted regions of the species range. Indeed, with heterosis (superiority of hybrids over parents) countering local inbreeding, the products of long-distance dispersal may be favoured by selection, at least in the first generation (Costa e Silva *et al.* 2014). Pollen dispersal may also enhance the adaptive response of the Tasmanian eucalypt flora through interspecific hybridization, however, this will only be an option for species within the same subgenus (Larcombe *et al.* 2015). Not only can introgressive hybridisation increase the genetic variance upon which selection can act (Kremer *et al.* 2012), but when seed-mediated dispersal is limited and endogenous reproductive barriers are weak, it may also play a role in enhancing gene and even species dispersal (Potts and Reid 1990). Indeed, the seed-mediated invasion of *E. risdonii* into the distribution of *E. amygdalina* described above appeared to

be heralded by a wave of hybridisation (Potts 1986). Not only are many boundary shifts likely to involve local asymmetric hybridisation, the process whereby a species may invade the range of another species through long-distance pollen dispersal and hybridisation has been long-recognised in *Eucalyptus* (Ashton 1976; Potts and Reid 1990) and *Quercus* (Petit *et al.* 2004). In this case, the invading pollen species may then be resurrected by selection from a segregating hybrid population and repeated backcrossing. This process of hybridisation and species resurrection may be an important dispersal mechanism by which a fitter pollen species could expand or shift its range by using a maladapted species from the same subgenus as a conduit into future suitable habitat.

While seed- and pollen-mediated dispersal may be limited in eucalypts (Booth 2017b), it proved to be an important consideration when estimating the future effectiveness of the Tasmanian reserve estate to conserve eucalypt populations under future climate change. Currently, hotspots of eucalypt diversity are well maintained within reserves, and it appears these reserves will remain as future climate 'safe havens' (Keppel *et al.* 2012; Gavin *et al.* 2014) for eucalypt diversity despite the modelled predictions of significant decreases in diversity under future climates. Our approach to use the proportion of a species occurrences within suitable habitat showed spatial changes in biodiversity may not be uniform, and suggests a more dynamical approach to conservation priorities may be required (Alagador *et al.* 2014). The decline of species can occur extremely quick (i.e. *E. morrisbyi* and *E. gunnii*), and while not all species can be conserved and many may need some form of assisted migration/colonisation (Aitken *et al.* 2008; Aitken and Whitlock 2013), our study provides a framework that could inform the prioritisation of climate-adjusted conservation strategies. For example, the identification of populations least at risk under future climates could provide the basis for *in situ* conservation actions. These populations will not only provide long-term occupancy of the species in the landscape under future climates but also key seed sources for *ex situ* strategies such as reforestation and ecological restoration. Alternatively, the identification of populations at risk of

maladaptation under future climates provides a prioritisation of areas for seed collections and possible seedbanking to capture genetic resources and diversity before break-down of the regeneration niche (see above).

In conclusion, this study has shown that the potential impact of climate change on the Tasmanian eucalypts may be extensive and non-random, however, large components of diversity will be well maintained in current reserve systems. While it must not be forgotten that these results are only a simulation of one potential outcome under future climate change and have many limitations (Araujo and Peterson 2012), it is most likely that these species will persist for a time in unsuitable habitat owing to their longevity and ability to regenerate following damage to the main stem. Nevertheless, the directionality of the predicted range shifts under future climate change presented here is consistent with currently observed boundary contractions (*E. gunnii*; Potts *et al.* 2001; Calder and Kirkpatrick 2008; Sanger *et al.* 2011), and expansions (*E. risdonii*; Potts 1986). The management of gene pools under climate change may require a paradigm shift in prioritising conservation efforts, with a greater focus towards *in situ* conservation of populations found in future suitable habitat while capturing genetic resources (seeds) from populations outside modelled suitable habitat and at risk of maladaptation for *ex situ* conservation strategies and ecological restoration. Such an approach is likely to give species the greatest chance for long-term survival under future climate change.

Acknowledgments

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Chapter 3: Planning for emerging novel ecosystems using habitat suitability models: the case for the Midlands of Tasmania, Australia

Abstract

Ecosystems provide important functions and services for humanity, however, mounting pressures from global change (land-use and climate change) are degrading their functionality. Global initiatives are using ecological restoration as one means of curtailing the current and future impact of global change on ecosystems. However, an outstanding challenge in ecological restoration is species choice. While the 'local-is-best' paradigm prevails in ecological restoration, continued shifts in selective regimes (i.e. climate) will likely increase the maladaptation risk of local species. Indeed, non-local species (i.e. emerging ecosystems) may be required when using only local species (traditional restoration) is unlikely to restore ecosystem functioning. To assist in guiding species choice, we propose a two-stage filtering process to model the habitat suitability of regionally local and non-local species across space and time under a high greenhouse gas emission climate change scenario. The application of this approach was demonstrated using the highly modified environment of the Midlands region on the island of Tasmania, Australia. While the choice of species for ecological restoration was predicted to vary through time, few local species were consistently predicted as suitable for ecological restoration, which was most evident for in the northern areas of the Midlands. Nevertheless, the expansion of suitable habitat for species not local to these northern areas was predicted. This case study highlights the potential of non-local species as candidates to restore ecosystem functionality and the importance in planning for the spatiotemporal change in species suitability for ecological restoration in future environments.

3.1 Introduction

Land-use change and increased globalisation have had enduring effects on vital ecosystem functions and services (Hobbs *et al.* 2009; Ellis *et al.* 2013). Indeed, the anthropogenic fingerprint is ubiquitous across both terrestrial and aquatic ecosystems (Scheffer *et al.* 2001; Foley *et al.* 2005; Chislock *et al.* 2013). Global initiatives such as the Bonn Challenge are attempting to curtail these effects by using ecological restoration as a conduit to restore 350 million hectares across the terrestrial biome by 2030 (http://www.bonnchallenge.org/). While ecological restoration aims to recover degraded, damaged, or destroyed ecosystems to some historical reference state (Balaguer *et al.* 2014; McDonald *et al.* 2016), the historical standpoint may be hard to define (Davis 2000), let alone hard to achieve and may be unsuitable under future climate change (Harris *et al.* 2006). The restoration of ecosystems will be complex and challenging, especially if community assemblages rearrange as species move upslope and to higher latitudes under climate change (Chen *et al.* 2011). Thus, there has been an increasing call to broaden the view of restoration to consider facets of emerging ecosystems that promote resilience to ongoing flux in the environment whilst maintaining and maximising ecosystem functioning (Hobbs *et al.* 2006; Seastedt *et al.* 2008; Perring *et al.* 2013).

An emerging ecosystem is one that has a unique composition of species which have not previously co-occurred together within a biome (Milton 2003). This could conceptually consist of the mix of native, regionally local and non-local species ('novel restoration') to produce a novel ecosystem that performs historical processes (Hobbs *et al.* 2006; Lindenmayer *et al.* 2008; Belnap *et al.* 2012). While it is likely some ecosystems may recover functionality using traditional restoration practices (e.g. utilising local species) (Barral *et al.* 2015), it is equally likely some ecosystems may require more proactive approaches (i.e. non-historical approach) through ecosystem engineering (Jackson and Hobbs 2009). Uncertainty in future climate projections will complicate the choice between traditional and novel restoration approaches. Nevertheless, simple extensions of habitat

suitability models (also known as ecological niche models and species distribution models) may provide a tool to guide the decision process. These models draw on ecological niche theory (Hutchinson 1957) and statistical relationships between the spatial distribution of a species and environmental variables to predict areas of suitable habitat. Although habitat suitability models have many known limitations (Pearson and Dawson 2003; Sinclair *et al.* 2010; Araujo and Peterson 2012), they have gained popularity for tackling a wide variety of conservation planning issues (Rose and Burton 2009; Franklin 2013; Guisan *et al.* 2013; Hamann and Aitken 2013).

Here, we propose a criteria-based approach that incorporates models of habitat suitability with an assessment of susceptibility to climate to track the spatiotemporal change in the choice of species for ecological restoration under future climates (Figure 3.1). This approach not only provides a method to guide the choice of local and non-local species for ecological restoration in a region, but also provides a valuable research framework to experimentally test various species choices. To demonstrate our approach for selecting species for ecological restoration, we used the Midlands region of the island of Tasmania, Australia, as a case study. The Midlands is an ideal study region as the landscape has a mosaic of patchy native woodland and grassland remnants of various levels of degradation within an extensive agricultural matrix (Fensham 1989). The Midlands is currently the focus of large-scale restoration projects where research trials have been embedded within the broader ecological plantings to test various species mixes and seed sourcing strategies (Bailey *et al.* 2013). While undertaking this study, we determined (i) whether the climate of the Midlands has changed since the detection of industrial warming in the Southern Hemisphere (Abrams *et al.* 2016), and (ii) whether the climate of the Midlands will change under future climate warming.

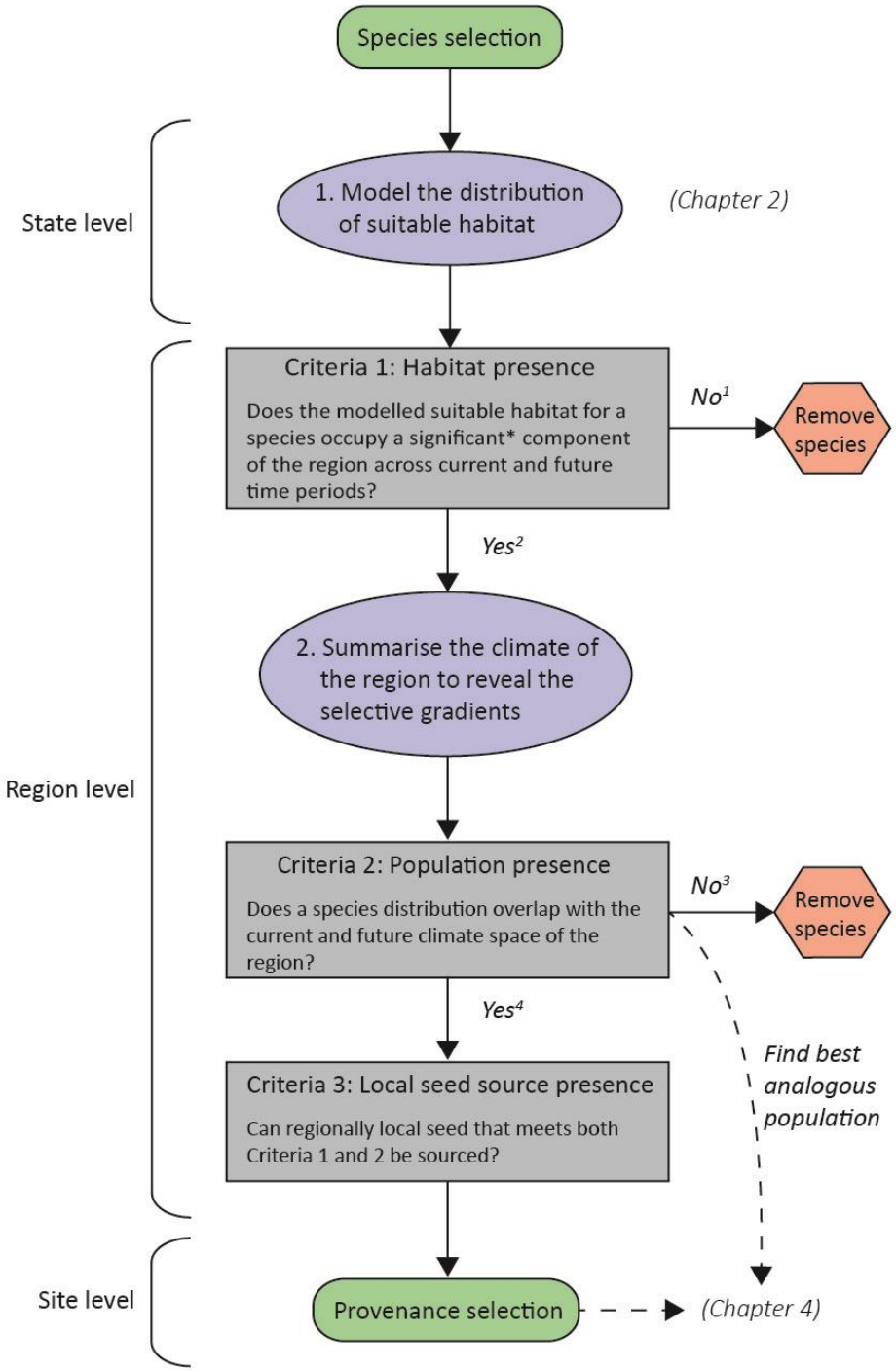

Figure 3.1. Conceptual framework to identify species best suited to a region under current and future environments. The first step is to model the distribution of suitable habitat for a species. These models are then used as the first filter to remove species that are not predicted to have a significant component of suitable habitat in the study region across current and future time periods. The second step is to then summaries the environmental variation occurring across the study region to reveal the underlying selective gradients. A second filter is then applied by removing species that do not remain in the current and future projected environmental space of the study region. A third filter is the applied to determine whether regional locl seed can be sourced by spatially mapping provenances that meet Criteria 1 and 2. Footnote: * A greater than 10% threshold was used to quantify whether a species had 'significant' suitable habitat area within the Midlands region.

3.2 Material and Methods

3.2.1 Conceptual approach to identify candidate species for restoration

This study focuses on the second ('Regional') level of our approach to select candidate species for ecological restoration. ('State' levels are covered in Chapter 2 and 'site' levels are covered in Chapter 4). Candidate species are filtered using three selection criteria (Figure 3.1). The first criteria filters species based on the proportion of their modelled suitable habitat that is contained within the study region through time (Figure 3.1). Species that do not have a significant component of their suitable habitat within the region are removed. The level of significance is based on an arbitrary threshold that is determined by the average area occupied by the species within the study region across the different time sequences (i.e. current and future). Species that meet this criterion are then passed through a second filtering criteria (Figure 3.1). This step firstly summarises the multidimensional climate space within a study region using a principal component analysis (PCA) to reveal the underlying orthogonal climate gradients. Species are added to this multidimensional climate space using the linear equation from the PCA to then quantify the percent of a species current occurrence that remain within the current and future climate space of the region. The third filtering criteria then determines whether regionally local seed that meets Criteria 1 and 2 can be sourced (Figure 3.1). For each time sequence, occurrences that are within the climate space of the region are spatially mapped and used to create an α convex hull (the smallest polygon containing a finite set of points) that identifies areas within a region that meet Criteria 1 and 2 to determine whether regionally local seed can be sourced.

3.2.2 The case of the Tasmanian Midlands

3.2.2.1 Study region

The Tasmanian Midlands is a biodiversity hotspot that encompasses the lowlands and foothills between the Eastern and Western Tiers from Launceston in the north to Hobart in the south (Whitten

et al. 2011; Figure 3.2). This region covers two biogeographic regions that share similarities in geology and ecology (northern Midlands and South-East, https://www.environment.gov.au/land/nrs/science/ibra). The topography of the Midlands is not as rugged as the rest of the island, however, the landscape becomes increasingly complex with decreasing latitude (Figure 3.2). Soils are generally nutrient-poor, however, pockets of more fertile soils over Jurassic and Carboniferous-Triassic sediments are common (Reid et al 2005). The Midlands is the most arid region on the island (mean annual precipitation, 472 – 761 mm^{-1}) and often experiences hot summers (mean maximum summer temperatures, 20.2 – 24.6 °C) with severe frost events occurring anytime throughout the year (Jackson 2005).

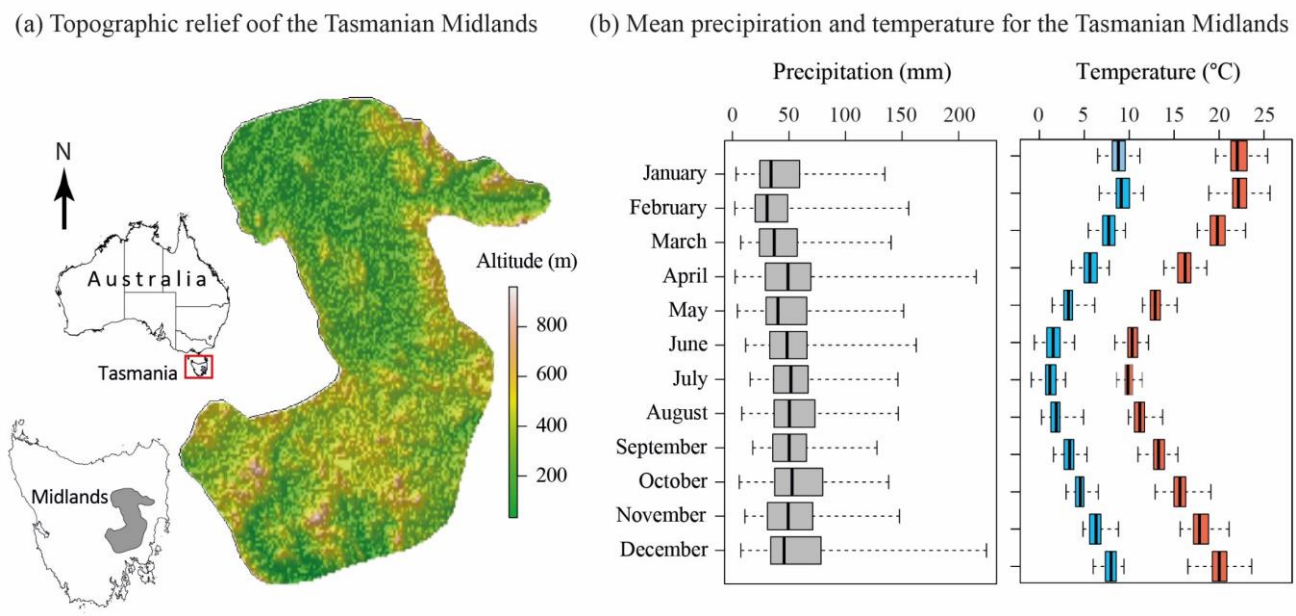

Figure 3.2. The geographic location of Tasmania (red box) relative to the mainland of Australia, and the Tasmanian Midlands showing the topographic relief across this region (a). Also shown is the monthly range in minimum (blue boxes) and maximum (red boxes) temperatures and precipitation (grey boxes) for the Midlands of Tasmania based on the average of 279 uniform points sampled across the Midlands (distance between points was 5 km) (b). The boxplots show the median (black line) and the upper and lower monthly range calcualed using gridded daily climate data (Jones *et al.* 2009) for the last 106 years (1911-2016).

The semi-arid climate of the Midlands supports a mix of dry sclerophyll woodlands and *Poa* grasslands. Many of the temperate woodlands and grasslands are threatened community types

(*National Conversation Act* 2002) that are now remnants embedded within the agricultural landscape. The Tasmanian temperate woodlands are dominated by tree species from the genus *Eucalyptus*. Tasmania has a diverse eucalypt flora with 30 species from two subgenera (*Symphyomyrtus* and *Eucalyptus*), and represents the southern-most extent of eucalypt distributions in Australia. Eucalypts are often the dominant tree of sclerophyllous ecosystems from near sea-level to the sub-alpine tree line. Across this altitudinal range, the island's eucalypts vary in form from tall trees (i.e. *E. regnans*) in wet forests, to a multi-stemmed mallees (*E. cordata*) in fire-prone forests, to a wind-pruned shrub (*E. vernicosa*) on mountain tops.

To identify candidate species for regional restoration in the Midlands, occurrence data for each eucalypt species in Tasmania were obtained from the Natural Values Atlas (http://www.naturalvaluesatlas.tas.gov.au/; accessed 6 February 2015), yielding 71,527 point occurrences. Duplicate occurrences and occurrences within 800 m of another were removed to limit the overrepresentation of a particular environment (Anderson and Gonzalez 2011). Spatial and environmental outliers were identified using a modified *z*-score test following Jordan *et al.* (2016) and were manually checked against known distribution descriptions and removed where appropriate. Three species (*Eucalyptus morrisbyi*, *E. nebulosa*, *E. perriniana*) were also removed due to their extreme rarity. This process yielded a final data set with 40,959 occurrence records.

3.2.2.2 Modelling the change in the Midlands climate over the last century

To determine whether the climate of the Midlands has significantly changed over the last century, daily minimum and maximum temperature and precipitation from the 1st January 1911 to 31st December 2016 (n = 38,717 days) were spatially extracted for 279 uniform points (spaced *ca.* 5 km apart) across the Midlands study region using topographically-adjusted rasters downloaded from the Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/, accessed 1st March 2017) at a spatial

resolution of 3 minutes (*ca.* 5 km) (Jones *et al.* 2009). To obtain an average daily climate dataset for the Midlands, we aggregated across the 279 points that were uniformly sampled over the region. Yearly temperature and precipitation bioclimatic variables were calculated following Xu and Hutchinson (2012) using the daily dataset and the 'getClimateVariables' function of the *AUSClim* package (P.A. Harrison, unpublished R package) in R (R Core Team 2016), setting the period argument to weekly. A multi-scalar drought index (standardised precipitation-evapotranspiration index, SPEI; Vicente-Serrano *et al.* 2010) was also calculated to detect past drought events and their severity, as well as to predict soil water deficit. To calculate SPEI we used a de-seasonalised 12-month accumulation of precipitation minus pan-evapotranspiration (PET) to calculate standardised departures of soil moisture availability (Vicente-Serrano *et al.* 2010; Cook *et al.* 2014). Pan-evapotranspiration was calculated using a modified (Hargreaves 1994) equation to correct for variation in monthly precipitation, which has been shown to significantly improve estimates of PET in arid environments (Droogers and Allen 2002). The SPEI and PET variables were calculated using the 'spei' and 'hargraves' function of the *SPEI* package (Vicente-Serrano *et al.* 2010) in R.

3.2.2.3 Identifying the key climate gradients across the Midlands

Regional climate rasters representing contemporary and future temperature and precipitation patterns across the island of Tasmania at a spatial resolution of 30 seconds (*ca.* 0.8 km) were obtained from the Climate Futures for Tasmania project (Corney *et al.* 2010) to identify the key climate gradients across the Midlands and predict how these gradient may change under future climate change. The baseline (1976-2005, hereafter 'current') climate surfaces were developed using ANUCLIM version 6.1 (Xu and Hutchinson 2012) which calculated 19 topographic-adjusted climate variables (Appendix B1). Future projections of these variables were obtained from a dynamically downscaled model using six GCMs (ECHAM5/MPI-OM, CSIRO Mk 3.5, GFDL-CM2.0, UKMO HadCM 3, GFDL-CM2.1 and MIROC3.2 (medres); Table 3.1) for three future time periods that

represented the 30-year average of 2010-2039, 2040–2069, and 2070–2099 (hereafter 2020s, 2050s, and 2080s) (see Corney *et al.* 2010 for further details). The six GCMs were selected by Corney *et al.* (2010) as they reasonably replicated current patterns in temperature and precipitation across south-eastern Australia, and also modelled credible representations of the El Niño Southern Oscillation (Smith and Chandler 2010). The future climate projections were developed assuming a high greenhouse gas emission and minimal mitigation scenario (SERS A2, IPCC 2013). While this is an extreme scenario, it represents a conservative approach when modelling a species response under climate change, despite current emission trajectories tracking the upper bounds of the A2 scenario (Peters *et al.* 2013) notwithstanding a recent plateau (Jackson *et al.* 2016).

Table 3.1. The six global circulation models (GCMs) used in the current study, country where they were developed, and the mean observed and 2080s projected change by the six GCMs for maximum temperature of the warmest week (TMXWW) and mean annual precipitation (RANN) for the Midlands of Tasmania. Change in RANN is expressed as a percentage increase/decrease relative to current.

Global circulation model	Country	Reference	TMXWW (°C)	RANN (%)
		Current (1976-2005)	22.7	585
CSIRO Mk 3.5	Australia	Gordon *et al.* (2010)	+2.5	+0.5
ECHAM5/MPI-OM	Germany	Stevens *et al.* (2013)	+2.2	+2.6
GFDL-CM2.0	USA	Delworth *et al.* (2006)	+2.5	+2.9
GFDL-CM2.1	USA	Delworth *et al.* (2006)	+2.3	+1.3
MIROC3.2(medres)	Japan	Abe-ouchi (2004)	+2.6	-0.4
UKMO HADCM3	United Kingdom	Johns *et al.* (2003)	+2.0	+7.1
		Grand mean	*+2.4*	*+2.3*

The key climate gradients across the Midlands was identified by firstly summarising the multidimensionality in the Midlands climate data using a PCA undertaken with the 'PCA' function of the *FactoMineR* package (Lê *et al.* 2008) in R. A PCA was used to summaries the climate variation of the Midlands as it is computationally quick and the output is easily interpretable. The PCA was calculated using a correlation matrix among the 19 climate variables that were centred and

standardised to a unit variance. Principal components (PCs) of the PCA were retained if the individual eigenvalue was greater than 1, which indicated that the PC axis accounted for more variation than a single variable alone (Quinn and Keough 2002). The retained PC axes were defined as the key climate gradients running across the Midlands and were characterised using the climate variable loadings (correlations) by selecting the most related (i.e. $|r|$ closest $r = 1$) temperature and precipitation variables that were also independent (i.e. $|r| < 0.5$) from the other PC axes.

3.2.2.4 Modelling the future climate envelope of the Midlands

To map the spatial and temporal redistribution of the climate envelope of the Midlands, we used the Random Forest algorithm (Breiman 2001) implemented in the *randomForest* package in R (Liaw and Weiner 2002), using the climate variables identified by the PCA (see above; Appendix B1). Random Forest is a machine-learning algorithm which creates a bootstrapped subsample of the original data to generate an ensemble of de-correlated regression trees. Random Forest was used as it is robust against over-fitting (Breiman 2001), can detect and handle complex non-linear relationships and interactions between predictor variables (Jones and Linder 2015; Wager and Walther 2016), as well as handling moderate levels of collinearity among predictor variables (Dormann *et al.* 2013). We grew 1000 trees using 6970 uniform points (30 sec grid points) sampled across the Midlands, with a balanced number of pseudo-absences randomly sampled across the environmental space of Tasmania. Following Breiman (2001), the number of randomly selected predictor variables (*mtry*) used as candidates for splitting a node was optimised by fitting preliminary models with (i) $mtry = (p/3) \times 0.5$, (ii) $mtry = p/3$, and (iii) $mtry = (p/3) \times 2$, where p is the number of predictor variables in the variable set X. The optimal value for *mtry* was determined as the model that (i) minimised the predictive error in the model using the mean squared error calculated as the sum of the squared differences between the ith observation in y and the average of the out-of-bag (OOB, samples excluded from the bootstrapped subsample) prediction for y_i, multiplied by the inverse of the

sample size *n* (Liaw and Wiener 2002), and (ii) maximised the discrimination power of the model using the Gini Index calculated as Gini = $2 \times (AUC - 0.5)$, where AUC is the area under the receiver-operating curve (Engler *et al.* 2004), and ranged from 0 (model is uninformative) to 1 (model perfectly discriminates). The Gini index was estimated for each species using a confusion matrix that was derived from a test data set (withheld 30% random sample of the data) that did not contribute to the training of the Random Forest model. The optimised model was predicted onto the contemporary and future climate surfaces (see above) to produce a spatial probability layer of habitat suitability (in this case, the Midlands climate envelope) using the *raster* package (Hijmans 2016) in R. Future predictions of suitable habitat were averaged across the six GCMs for each time step (2020s, 2050s, 2080s).

3.2.2.5 Identifying candidate species for the Midlands using the criteria-based framework

The total area of modelled suitable habitat for each of the 27 Tasmanian eucalypt species within the Midlands was quantified to determine which species met the requirement of Criteria 1 (Figure 3.1), using previously developed habitat suitability models (see section 2.2.4 of Chapter 2). Briefly, habitat suitability models were derived for each eucalypt species native to Tasmania using twelve predictor variables and the *randomForest* package in R to create a binary layer (0, not suitable; 1, suitable) that represented the spatial distribution of predicted suitable climate habitat under current and future climates in Tasmania. The habitat suitability surfaces were confined to the geographic extent of the Midlands region. The total area of suitable habitat for each species within the Midlands region ($AREA_{SPECIES}$) under current and future climates (2020s, 2050s, and 2080s) was calculated using the 'area' function of the *raster* package, and converted to the percent of the Midlands occupied ($AREA_{PERCENT} = (AREA_{SPECIES} / AREA_{REGION}) * 100$, where $AREA_{REGION} = 8388$ km^2). Species with predicted suitable habitat that occupied on average greater than 10% of the Midlands

region across the four time periods (current, 2020s, 2050s, 2080s) was determined to occupy a 'significant' component of the Midlands region.

Species that met Criteria 1 were then passed through the second filtering criteria (Criteria 2; Figure 3.1) to quantify the potential susceptibility (i.e. increased risk of maladaptation) of a species to future climate change in the Midlands. First, the PC scores for each species occurrence record were calculated using the PCA formula and the contemporary climate data. The percent of a species occurrences that fell within the current climate space of the Midlands provided the baseline percentage to estimate a species susceptibility. Second, the climate space of the Midlands was predicted into the future using the multi-model mean (average of six GCMs; Fordham *et al.* 2011) climate projections for the 2020s, 2050s, and 2080s, while keeping a species occurrence fixed to the contemporary (1979-2005) climate. The susceptibility of a species was quantified as the percent of its occurrences that fall within the future climate space of the Midlands relative to the baseline.

The occurrence records of a species that fell within the multidimensional climate space of the Midlands were identified and spatially mapped to determine whether geographically local seed to the Midlands could be sourced across the four time periods (current, 2020s, 2050s, 2080s) (Criteria 3; Figure 3.1). These mapped records represent real observations of a species within the Midlands region that were (i) within predicted suitable habitat for the species (based on models from Chapter 2), and (ii) within the climate space of the Midlands, at the mapped point in time. Areas of the Midlands that may be candidate seed sources for a species were visualised using an α convex hull ($\alpha = 0.1$) around the identified points undertaken with the 'ahull' function of the *alphahull* package (Pateiro-Lopez *et al.* 2016).

3.3 Results

3.3.1 The climate of the Midlands has changed over the past century

Over the past century the mean annual temperature across the Midlands region has increased by 0.7˚C (Figure 3.3). While patterns of annual precipitation have varied (range: 380 mm [2006] to 1000 mm [1916]), there was no evidence of a trend in precipitation despite a weak decrease in annual precipitation since 1996 (Figure 3.3). There was, however, a decreasing trend in the predicted soil moisture availability (i.e. SPEI), with only 11 of the last 41 years having surplus soil water content (Figure 3.3). A total of nine severe drought events (SPEI $\leq$ -1) have occurred in the Tasmanian Midlands since 1911, with three of these severe drought events occurring in the last decade (Figure 3.3). The longest drought event (SPEI < 0) occurred over a seven-year period between 2003 and 2009.

3.3.2 The climate of the Midlands is predicted to continue changing

The current climate space of the Midlands was summarised using three orthogonal axes which captured 91% of the variance in the climate data. The three axes corresponded to a summer (PC1) and winter (PC2) aridity gradient and a frost gradient (PC3) (Appendix B2; see Appendix B3 for further details). Projection of the Midlands climate space in the future (2020s, 2050s, 2050s) suggested an increase in summer and winter aridity and a decrease in the frequency of frosts (Figure 3.4; see Appendix B4 for further details). The projected warming of the Midlands through time is predicted shift the current climate envelope of the Midlands in a westward and upslope direction onto the Central Plateau of Tasmania (Figure 3.5; see Appendix B5 for further details).

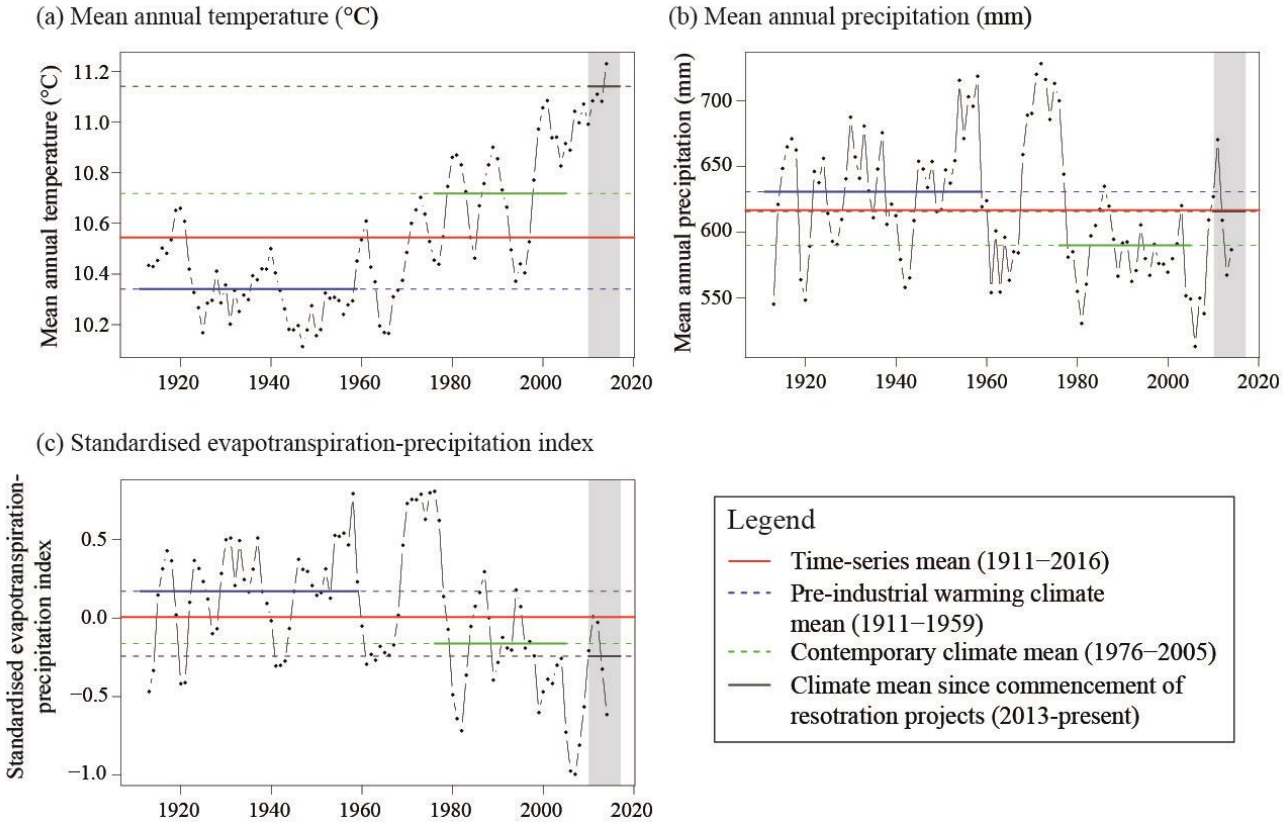

Figure 3.3. Mean climate data for the Midlands of Tasmania from 1911 to 2016. Daily climate data was downloaded from The Australian Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/, accessed 1st March 2017; Jones *et al*. 2009) for 279 uniform points sampled across the Midlands (distance between points was 5 km) then aggregated. The daily data was used to calculate (a) mean annual temperature, (b) mean annual precipitation, and (c) the standardised precipitation-evapotranspiration index (SPEI; Vincente-Serrano *et al*. 2010). The solid black line represents the trend in the data based on a 5 year moving average window. Four averages were calculated: (i) the grand-mean across the 106 year period (red line), (ii) the mean during the time period (1911-1959) before the detection of anthropogenic climate change in the Southern Hemisphere (Abram *et al*. 2016) (blue line), (iii) the mean during the time period (1976-2005) considered as baseline contemporary climate (Xu and Hutchinson 2012) (green line), (iv) the mean climate since the commencement of restoration projects in the Midlands (Bailey *et al.* 2013) (grey line).

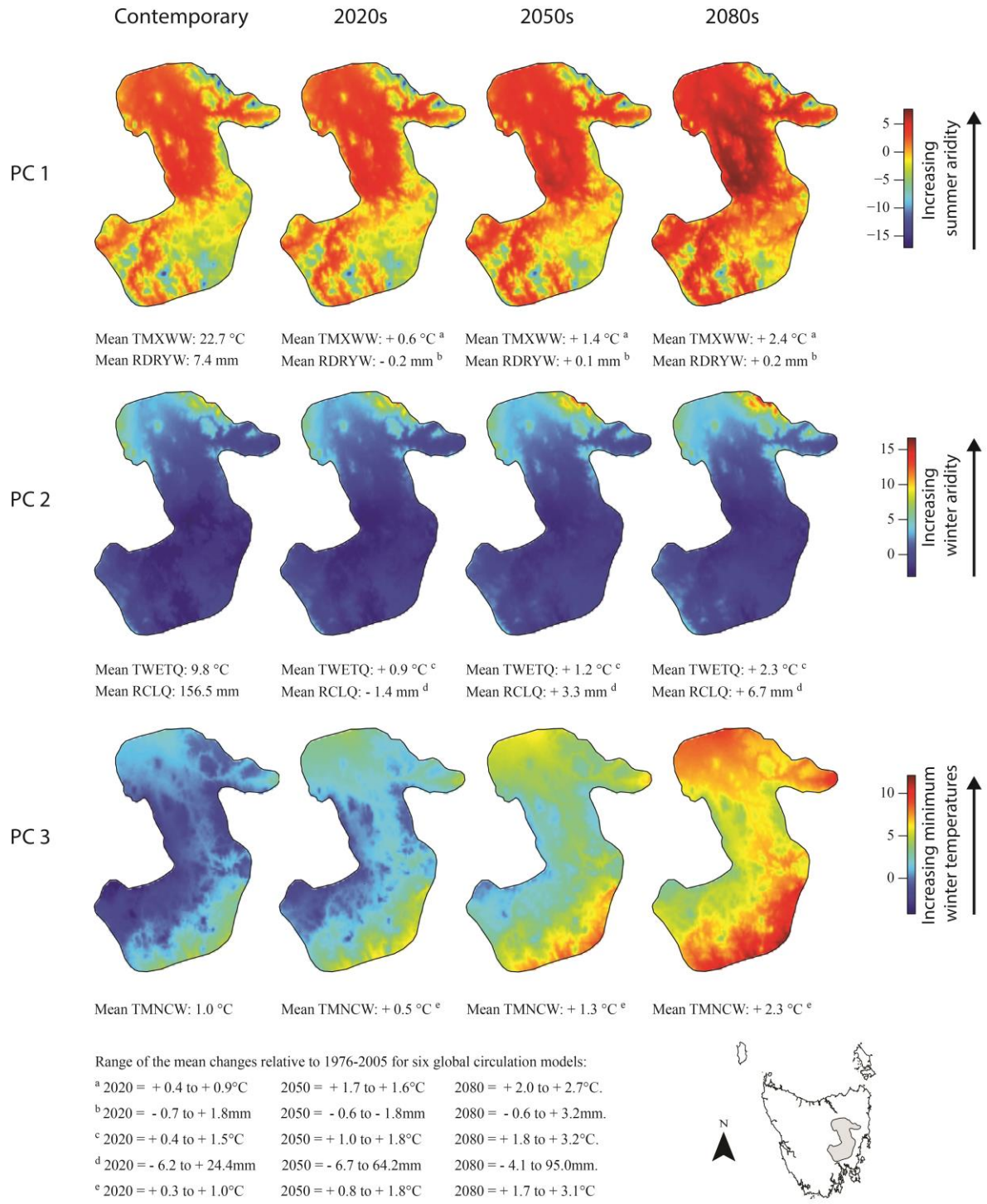

Figure 3.4. The spatiotemporal change in contemporary (1976-2005) and future climates (2020s, 2050s, 2080s) across the Tasmanian Midlands based on the three principal components (PC) from the principal components analysis (PCA). Also shown under each plot are the relative change in the key climate variables that best explained the PC axis. Increasing values along PC1 and PC2 (cool to warm colours) correspond with increases in summer and winter aridity, respectively. Increasing values along PC3 (cool to warm) indicates warming of minimum winter temperatures which is likely associated with a decrease in forest prevelance. (Maximum temperature of the warmest week, TMXWW; precipitation of the driest week, RDRYW; temperature of the wettest quarter, TWETQ; precipitation of the coldest quarter, RCLQ; minimum temperature of the coldest week, TMNCW).

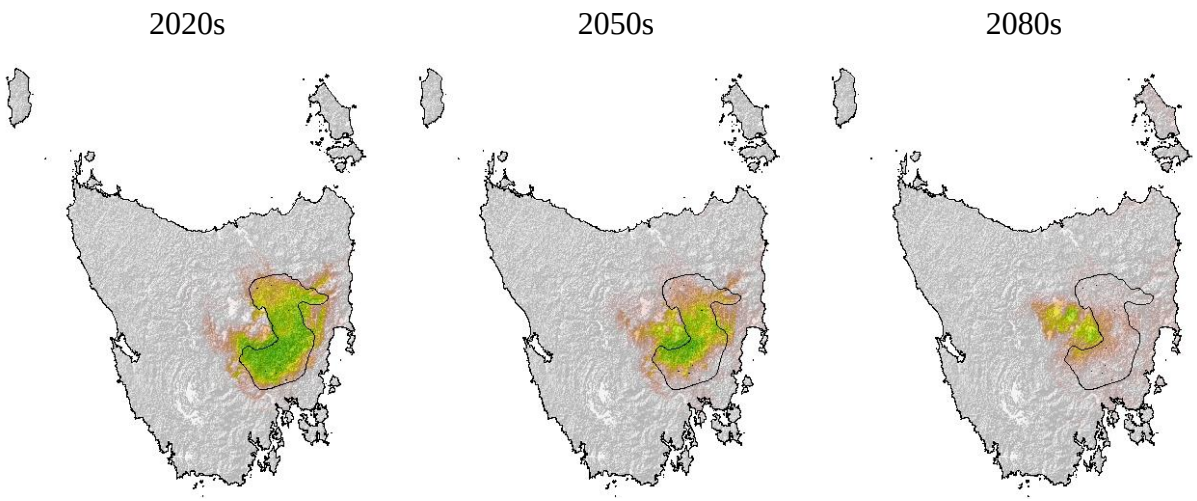

Figure 3.5. The predicted distribution of the future (2020s, 2050s, 2080s) climate envelope of the Midlands. The change in the Midlands climate envelope was modelled using the six climate variables identified by the principal components analysis (PCA) (maximum temperature of the warmest week, precipitation of the driest week, temperature of the wettest quarter, precipitation of the coldest quarter, minimum temperature of the coldest week). The surface corresponds to the probability of a 1 km grid cell containing suitable climate habitat, ranging from dark-green indicated the highest probability (1) of suitable habitat, to grey indicating the lowest probability (0) of suitable habitat.

3.3.3 Identifying candidate eucalypt species for restoration in the Midlands region

3.3.2 Criteria 1: habitat presence

Most of the Tasmanian eucalypt species were predicted to have a component of their current modelled suitable habitat within the Midlands (range: 0 % to 69 %; Table 3.2; Appendix B6). After applying Criteria 1 of our framework (Figure 3.1), 11 of the 27 eucalypt species maintained a 'significant' (> 10%) component of their modelled suitable habitat within the Midlands across the four study periods (current [1976-2005], 2020s, 2050s, 2080s) (Table 3.2). *Eucalyptus ovata* (96%) and *E. amygdalina* (46%) were predicted to have the largest area of suitable habitat within the Midlands by the end of this century, while *E. rubida* showed the greatest reduction in predicted area occupied through time (Table 3.2). Most of the 11 species were local to the Midlands region, with the exception being the non-local species *E. risdonii*.

Table 3.2. Percent area of the Midlands (area = 6388 km^2) predicted to contain modelled suitable habitat under current (1975-2005) and future (2020s, 2050s, and 2080s) climates. Species are alphabetically ranked and the asterisk symbol corresponds to the 11 species that met Criteria 1 (i.e. containing a 'significant' (e.g. > 10%) percent area of suitable habitat within the Midlands).

Species	Suitable habitat within Midlands (% area)			
	Current	2020s	2050s	2080s
E. amygdalina *	34.7	27.7	39.5	46.2
E. archeri	0.1	0	0	0
E. barberi *	11.6	10.4	15.1	8.7
E. brookeriana	9.7	3.6	0.9	0.2
E. coccifera	1.7	0.3	0	0
E. cordata	1.7	0.7	1.7	0.5
E. dalrympleana	19.6	6.8	1.4	0
E. delegatensis	11.6	4.4	0.9	0.2
E. globulus *	17.9	19.3	25.7	10.2
E. gunnii	0.2	0	0	0
E. johnstonii	0.1	0	0	0
E. nitida	0	0	0	0
E. obliqua	7.7	3.8	2.5	1.7
E. ovata *	64.8	74.8	92.3	96.3
E. pauciflora *	75	49.9	10	0
E. pulchella *	29.2	35.5	46.4	45.4
E. radiata	0	0	0	0
E. regnans	2	0.4	0.2	0.5
E. risdonii *	6	11.3	44.5	55.9
E. rodwayi *	48	34.7	5	7
E. rubida *	69.3	58.2	41.6	20.2
E. sieberi	2.6	2.5	1	4.2
E. subcrenulata	0	0	0	0
E. tenuiramis *	38	25.4	38.2	35.4
E. urnigera	1.4	0.1	0.1	0.1
E. vernicosa	0	0	0	0
E. viminalis *	46.2	37.7	37.8	30.8

3.3.3 Criteria 2: population presence

The assessment of susceptibility found that the 11 species identified under Criteria 1 maintained a large percent of occurrence records within the current climate space of the Midlands (range: 26 % to 88%; Table 3.3). As the Midlands climate space shifted through time, most species (with the exception of *E pauciflora*, *E. rodwayi*, and *E. rubida*) tended to show an increase in the percent of

occurrences that fell within the future climate space of the Midlands (Appendix B7; Table 3.3).

Table 3.3. Assessment of susceptibility of the 11 eucalypt species showing the percent of occurrences for species that fall within the Midlands multidimensional climate space under current (1976-2005) and future (2020s, 2050s, 2080s) climates.

Species	Percent species occurrences in Midlands climate space			
	Current	2020s	2050s	2080s
E. amygdalina	33.8	43.6	59.6	58.8
E. barberi	56.9	70.6	94.8	77.8
E. globulus	26.4	39.5	50.8	58.1
E. ovata	34.6	45.7	53.2	51.8
E. pauciflora	70.4	66.3	41.5	11.9
E. pulchella	41.5	60.3	70.1	68.9
E. risdonii	54.8	71.4	59.5	51.2
E. rodwayi	52	54.1	37.6	21
E. rubida	88.1	79.5	59.9	23.1
E. tenuiramis	43.6	53.8	55.2	53.9
E. viminalis	37.5	48.8	59.4	55

3.3.4 Criteria 3: Local seed source presence

A large proportion of a species occurrences that overlapped with the current climate space of the Midlands (e.g. Appendix B7) tended to also be geographically local to the Midlands (Appendix B8). This was visualised using an α convex hull around these identified occurrences and represents locations that met Criteria 1 and 2 (green surface - Figure 3.6 and Appendix B9). The spatial distribution of these locations under current climates had a certain degree of consistency, with most of the southern Midlands maintaining the greatest area of suitable habitat and local populations within the current climate space of the Midlands (Figure 3.6). *Eucalyptus ovata* (52%), *E. pauciflora* (45%) and *E. viminalis* (40%) had the largest area across the Midlands region that met Criteria 1 and 2 under current climate conditions (Figure 3.6; Appendix B8).

While the shift in the Midlands climate space under future climate change tended to result in an increase in the overlap with a species' occurrences through time (Table3.3), most of these

occurrences tended to be located outside the geographic extent of the Midlands (Appendix B8). Indeed, by the end of this century (i.e. 2080s) all species had less than 1% of the total Midlands area that met both Criteria 1 and 2 (Appendix B8), with *E. amygdalina* (0.9%) and *E. ovata* (0.8%) the main species that were predicted to maintain local provenances in the Midlands (Figure 3.6; Appendix B9). Nevertheless, the Midlands continued to maintain modelled suitable habitat for most species by the end of the century, with the exception of *E. pauciflora* (orange polygon - Figure 3.6; Appendix B8), indicating these locally occurring species were predicted to be suitable for restoration projects in this region, however, non-local seed sources may be required in the future. While the future climate of the northern Midlands was predicted to be outside most of the 11 candidate species modelled suitable habitat, the regionally non-local species *E. risdonii* was predicted to expand its distribution of suitable habitat from the southern Midlands to the northern Midlands through time (Figure 3.6; Appendix B8).

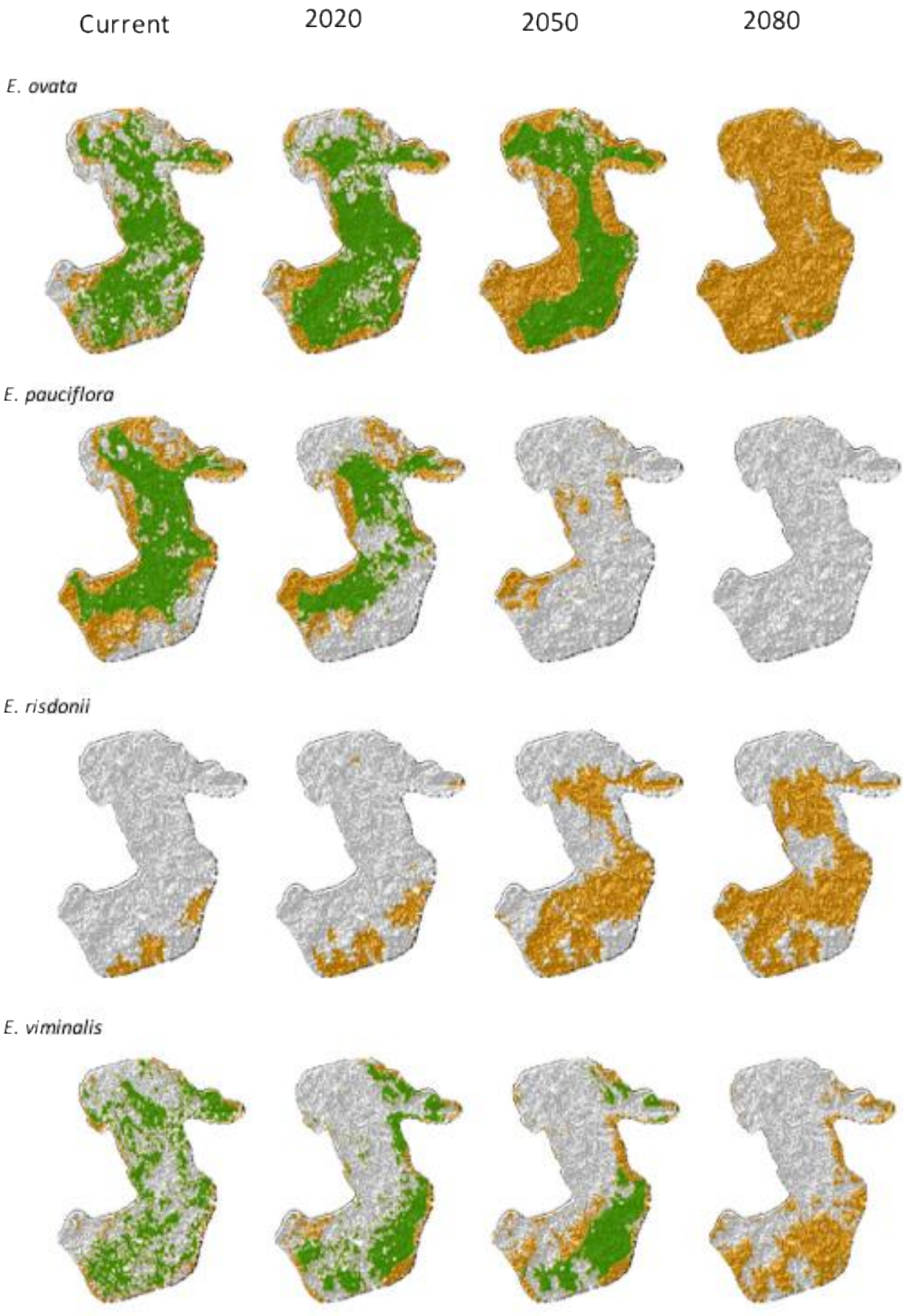
Current
2020
2050
2080
E. ovata
E. pauciflora
E. risdonii
E. viminalis

Figure 3.6 (page 78). Predicted distribution of suitable habitat (combined green and orange surfaces) modelled under current (1976-2005) and future (2020s, 2050s, 2080s) climates for a subsample of the 11 Tasmanian eucalypts identified using Criteria 1 (see Appendix B9 for maps of the remaining seven species). The orange surface shows areas that are predicted to be suitable habitat for a species but no known occurrences were identified as overlapping with the climate space (i.e. PCA space) of the Midlands for that mapped time period. The green surface represents the α convex hull and shows areas that are predicted to be suitable habitat for a species and contain known occurrences that were identified as overlapping with the climate space of the Midlands for that mapped time period. The white/grey surface represents areas that were not modelled as suitable for a species under current or future climate conditions of the Midlands.

3.4 Discussion

3.4.1 Climate of Midlands has changed and is projected to continue changing

The climate of the Tasmanian Midlands has changed over the last 100 years. Mean annual temperatures have steadily increased by 0.7 °C across this region since the emergence of pre-industrial warming in the Southern Hemisphere (Abram *et al.* 2016). The observed increase in mean annual temperature is consistent with trends across Australia (CSIRO and Bureau of Meteorology 2015) and the global average of 0.85 °C (IPCC 2014). The climate of the Midlands has also become increasingly dry (i.e. reduced soil water) over the last 40 years. The significant increase in temperatures coupled with variable but consistent precipitation patterns has led to an increased evaporative demand, resulting in a significant drying effect across the Midlands region. Increasing dryness is a global phenomenon (Dai 2013; Sherwood and Fu 2014) and is thought to have contributed to the expansion of grasslands and savanna woodlands over the past 60 years (Feng and Fu 2013). Nevertheless, temperature-driven aridity (coupled with multi-decadal variability in the Indian Ocean Dipole) has been attributed to one of the worst drought events in Australia's recent history - termed the Millennium Drought (Ummenhofer *et al.* 2009; Verdon-Kidd and Kiem 2009; Gergis *et al.* 2012). The Millennium Drought led to extensive tree deaths (Semple *et al.* 2010) and similar drought events have had a widespread impact on forest ecosystems (Jurskis 2005; Fensham *et al.* 2009; Allen *et al.* 2010; Williams *et al.* 2010). Indeed, drought-induced water stress has been coincidently linked with rural tree decline across the Tasmanian Midlands (Neyland 1996; Close and Davidson 2004). While future forest dieback will be difficult to predict (Allen 2009), the continued

drying of the Tasmanian Midlands under future climates is likely to result in the quick on-set of intense droughts (Dai 2013; Trenberth *et al.* 2014), which will likely impose additional stress on remnant vegetation across this modified landscape (Allen *et al.* 2010). Indeed, future climate predictions argue for a decrease in broad-scale forest canopy cover in the Midlands region (Williamson *et al.* 2014).

The climate of the Tasmanian Midlands is projected to continue changing and become much warmer than present. The projected rise in temperature and relatively unchanged precipitation regimes across the Midlands region are generally consistent with other regional changes projected for Tasmania (Chapter 2; Corney *et al.* 2010). Indeed, the modelled redistribution of the climate envelope of the Midlands region onto the southern extents of the Central Highlands by the end of this century is consistent with current and projected warming and decreasing precipitation trends across the Central Highlands (Chapter 1; Sanger *et al.* 2011). While the projected rise in temperature for the Midlands region is comparable with projected trends across Australia, the future stability of precipitation patterns in the Midlands is not in accordance with the projected decrease in precipitation for southern and eastern Australia (CSIRO and Bureau of Meteorology 2015). Nevertheless, the future stability of precipitation patterns in the Midlands is consistent with global projections for similar mid-latitude regions (IPCC 2014). The inherent difficulties in projecting future precipitation regimes is evident from the high variability among GCMs (global circulation models). While we used GCMs that best replicated recent precipitation patterns across Australia (Smith and Chandler 2010), and that have been identified has 'most skillful' (Fordham *et al.* 2011), we used a multi-model approach to further account for the uncertainty in future precipitation patterns (Fordham *et al.* 2011; Schaller *et al.* 2011). While this cautious approach may not represent a plausible future scenario, it nevertheless provides a conservative and robust projection of future climates when deciding on candidate species for ecological restoration.

3.4.2 Regional species choice for ecological restoration

Our two-step procedure to select species for ecological restoration identified eleven candidate species based on models of habitat suitability (Criteria 1) and climate susceptibility (Criteria 2). The use of habitat suitability models have gained increased popularity among conservation ecologists (Rose and Burton 2009; Guisan *et al.* 2013), and have been important in guiding species translocations under future climate change scenarios (Gray and Hamann 2011, 2013; Gray *et al.* 2011). Nevertheless, relatively few studies have expanded the use of habitat suitability models to inform species choice for ecological restoration (Booth *et al.* 2012; Gelviz-Gelvez *et al.* 2015; López-Tirado and Hidalgo 2015; Butterfield *et al.* 2016). This may perhaps be partly due to the entrenched paradigm that 'local-is-best' (Hancock and Hughes 2012).

The 'local-is-best' paradigm in ecological restoration presumes species have evolved local adaptations that give them an evolutionary advantage over non-local species (Mortlock 2000; Johnson *et al.* 2010). While it is undeniable that species evolve adaptations to local selective gradients such as climate (Jump and Peñuelas 2005), a mean shift in the selective gradient under environmental flux will likely result in the decoupling of the local adaptations leading to an increased risk of maladaptation (Rehfeldt 1992; Rehfeldt *et al.* 2002). Indeed, land-use change (e.g. fragmentation of remnant habitat) and climate change may result in the overall reduction in local fitness (Leimu and Fischer 2008; Hancock and Hughes 2014). However, the challenge remains in testing whether provenances of non-local species will have an adaptive advantage over local species as novel environments emerge (Jones 2013b), and our two-step procedure provides a step towards planning and experimentally testing emerging ecosystems.

Of the eleven candidate species identified in this study, only one species (*E. risdonii*) was non-local. The northward expansion of modelled suitable habitat for *E. risdonii* through time was

expected given its current dominance of dry, drought-prone north-west facing slopes in south-eastern Tasmania (Kirkpatrick and Nunez 1980). Although a high frequency of species locally found in the Tasmanian Midlands region were identified as candidates for ecological restoration, the choice of species was non-uniform, with a notable spatiotemporal pattern. Indeed, under a warming Midlands climate, the habitat suitability models predicted the extensive displacement of suitable habitat for most species towards the southern Midlands. While it is likely restoration goals may be achieved using traditional restoration processes in the southern Midlands, more pragmatic strategies may be required for the northern Midlands. Indeed, by the end of this century only two locally found species (*E. ovata*, *E. amygdalina*) were predicted to maintain modelled suitable habitat within the northern Midlands. The loss of predicted habitat for local candidate species may be compensated by the modelled spatiotemporal expansion of the northern boundaries of *E. pulchella* and *E. risdonii* into the northern Midlands. However, these areas are well beyond the current distribution margins of these species, and the future occupancy within these areas would require assisted translocations (Thomas 2011; Lunt *et al.* 2013).

3.4.3 Planning for emerging ecosystem

The predicted changes in abiotic (i.e. climate) and biotic (i.e. eucalypt species) conditions of the northern Midlands, superimposed over nearly two centuries of agriculture activities (Fensham 1989), may make restoring to a historical composition of species moot under future environmental flux (Perring *et al.* 2013).Whether or not the northern Midlands follows a trajectory towards a novel ecosystem (i.e. an ecosystem that will not return to a historical state – Hobbs *et al.* 2006), the difficulty remains in how to recover historical functionality through ecosystem engineering whilst accounting for temporal changes in a species suitability. Bradshaw (1983) outlined the two general stages of ecosystem establishment and development. The first stage is the colonisation of denuded landscapes through immigration, selection and establishment of communities. This is then followed

by a second wave of immigration as soil structure develops by increased plant and animal activity, increased soil nutrient load, and reduce soil toxicities. Traditional ecological restoration conceptually exploits the first stage of ecosystem development through deliberate re-introduction of local species in degraded landscapes to reset trajectories towards the restoration goal (Millar *et al.* 2007). Taking an individualistic viewpoint of ecosystems (e.g. conceptualising communities as an assortment of individual species that share paralleled adaptations along an environmental gradient - Gleason 1926), the first stage of ecosystem development (see above) may be further manipulated at the micro-scale to engineer historical ecosystem functions using a unique composition of species that have not co-occurred in recent evolutionary time. For example, a mosaic of local and non-local species may be established at sites in the northern Midlands by planting the flood-prone *E. ovata* (local species) across low-lying habitats likely to hold water and *E. risdonii* (non-local species) across areas less likely to flood. Nevertheless, ecological and conservation ecologists will need to take heed of the unknown implications translocation may impose on surrounding remnant vegetation (McLachlan *et al.* 2007; Bucharova 2016), and the potential co-evolution between species that may be important for maximum fitness (Grady *et al.* 2016).

3.4.4 Need for targeted seed collections

As the climate of the Tasmanian Midlands changes, our results predict there will be variable, yet relatively extensive areas of suitable modelled habitat for most of the 11 candidate species identified in this study. However, by the end of this century, it is predicted that most of the local populations of these 11 species may be at risk of climate maladaptation. In many cases there will likely be non-local provenance of these species that would be better suited to the future environments of the Midlands region. Regardless of whether using local or non-local species for ecological restoration, the challenge remains in identifying the best seed sources (provenances) that will maximise the long-term climate-resilience of the plantings (Millar *et al.* 2007; Prober *et al.* 2016). While there are an

increasing number of strategies to guide the targeted collection of appropriate seed sources, for example along a spatiotemporal gradient of predicted environmental change (climate-adjusted provenancing - Prober *et al.* 2015), practical tools that implement such strategies for restoration and conservation ecologists are limited. Therefore, there is now an urgent need to develop tools that translate the concepts of different provenancing strategies into reality, and into the ready reach of practitioners.

Acknowledgements

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Chapter 4: Integrating climate change and habitat fragmentation to identify candidate seed sources for ecological restoration

Abstract

Anthropogenic change (climate change and habitat fragmentation) is driving a growing view that local seed collections may need to be supplemented with non-local seed as a strategy to bolster genetic diversity and thus increase evolutionary potential of plantings. While this strategy is becoming widely promoted, empirical support is limited, and there is a lack of accessible research tools to assist in its experimental testing. We therefore provide the Provenancing Using Climate Analogues (PUCA) framework that integrates the principles of the climate-adjusted provenancing strategy with concepts from population genetics (i.e. potential inbreeding in small fragmented populations) as both a research and operational-ready tool to guide the collection of non-local seed. We demonstrate the application of PUCA using the Midlands of Tasmania, Australia; a region that is currently undergoing large-scale ecological restoration. We highlight multiple non-local seed sources for testing by identifying actual species distribution records that currently occupy environments similar to that projected to occur at the restoration site in the future. We discuss the assumptions of PUCA and the ecological considerations that need to be tested when moving non-local genotypes across the landscape.

4.1 Introduction

An important question in ecological restoration is, "How do we identify provenances that will maximise resilience in the face of climate change?" Several approaches have been recently proposed with the view to increase resilience of restoration plantings by supplementing the local seed collections with non-local seed from more genetic diverse provenances (Broadhurst *et al.* 2008) or from provenances that may be best adapted to future climates (Sgrò *et al.* 2011; Breed *et al.* 2013; Prober *et al.* 2015). The recently proposed climate-adjusted provenancing strategy by Prober *et al*.

(2015) prescribes the supplementary collection of seed along a gradient of environmental change (i.e. climate change) associated with the restoration site. This is achieved by identifying provenances that currently occupy analogous environments projected for the restoration site through time, thus capturing the standing adaptations in non-local provenances and maintaining the *in situ* evolutionary potential of the local provenances. Whether the assumptions of this strategy are valid, however, requires the development of tools to identify such seed sources to allow for experimental testing.

The targeting of climate analogues is an emerging approach in both agriculture (Ramirez-Villegas *et al.* 2011) and restoration/reforestation (Gray and Hamann 2011; Booth 2016; but see Hancock *et al.* 2016). However, many identified seed sources may be growing in fragmented landscapes where seed quality and quantity may be compromised in small remnant populations by inbreeding and reduced pollinator activity (Ellstrand and Elam 1993; Young *et al.* 1996). Here, we outline the Provenancing Using Climate Analogues (PUCA) approach that integrates the principles of the climate-adjusted provenancing strategy with such population genetic considerations. We demonstrate the application of this novel framework to restoration sites in the Midlands of Tasmania, Australia, where we are experimentally testing various seed sourcing strategies (Bailey *et al.* 2013).

4.2 Material and methods

4.2.1 Identifying candidate seed sources

To identify candidate seed sources, the developed Provenancing Using Climate Analogues (PUCA) framework requires four datasets: (1) a target region that contains the restoration site, (2) environmental layers depicting the current (baseline) and future projections, (3) species distribution data, and (4) a habitat fragmentation layer. Hancock *et al*. (2016) provide a comprehensive list of resources (Australia-only) that can be used with PUCA, however, PUCA does provide the facilities

to acquire these datasets from global-scale databases (see Appendix C1). Here, we define the environment using only climate, however, additional facets of the environment (such as soil) can be easily added.

The generalised procedure of PUCA is shown in Figure 4.1. PUCA proceeds by firstly summarising the current climate variation occurring across the target region into fewer, meaningful components using a Principal Components Analysis (PCA). This results in a regional climate space that is multidimensional, with only significant components (i.e. dimensions) retained. The regional climate space is then truncated to a restricted geographical space around the restoration site (buffer, *w*), where *w* is typically expressed as a radius in kilometres and represents the generalised area of a local provenance. Species records are added into the truncated, regional climate space using the same climate layers and the linear equation from the PCA, resulting in the climate space of the species and region being on the same scale. This then allows for the identification of species records that occur in analogous current and future climates for the restoration site by calculating the Standardised Euclidean Distance (SED; Williams and Jackson 2007) between the truncated, regional climate space and each species record. A user-defined threshold on the SED is then applied to identify the species records best aligned with the restoration site. The habitat fragmentation layer is used to identify which records occur in anthropogenically disturbed landscapes. The PUCA framework is conveniently packaged as an R library which is available from https://github.com/peteraharrison/PUCA. A demonstration of the PUCA R library (and acknowledgment of several R packages that made this tool possible) is given in Appendix C1.

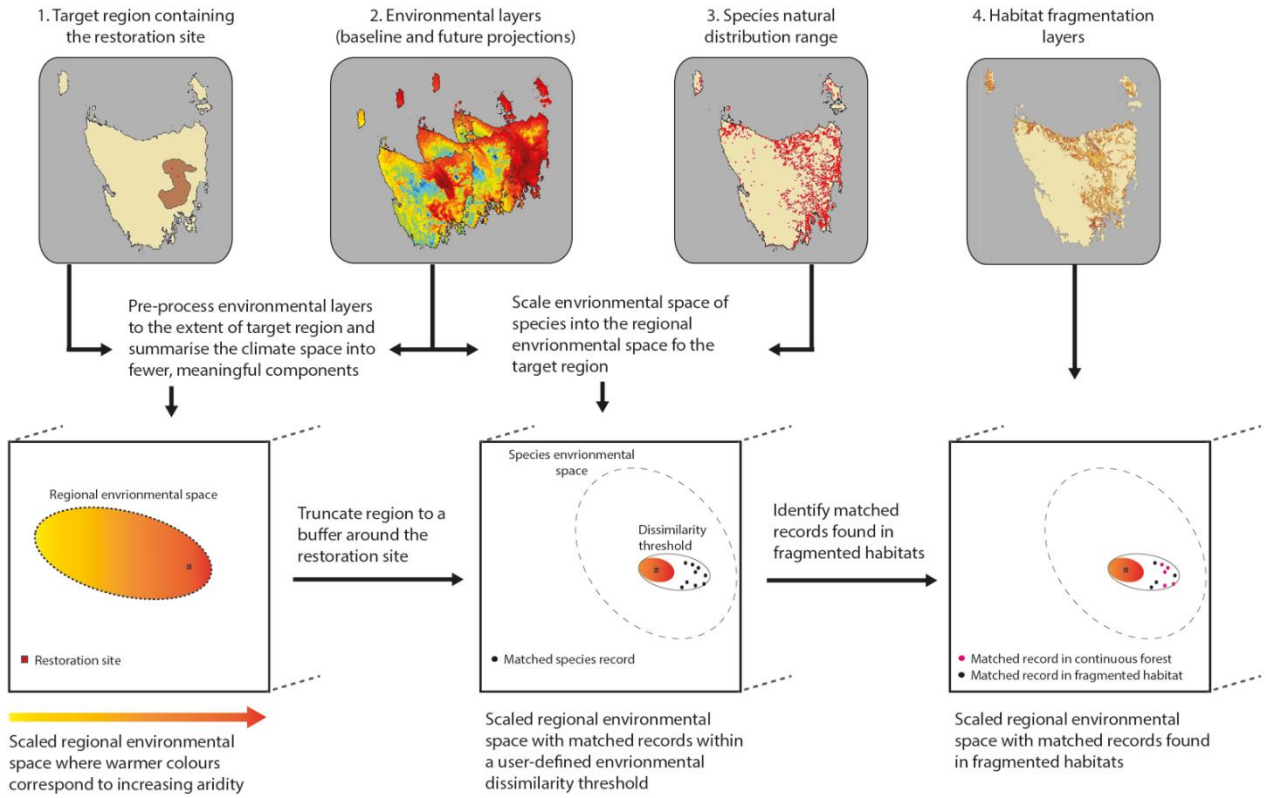

Figure 4.1. Generalized procedure of the Provenancing Using Climate Analogues (PUCA) framework. Shown are the four required datasets for PUCA to identify species records that are most analogous to the current and future climate for the restoration site by first summarizing the environmental variation of a region into fewer, meaningful components, then truncating the regional environmental space to a geographical buffer around the restoration site to limit the search area to match species records with the restoration site. The habitat fragmentation layer is then used to identify which matched species records occur in disturbed landscapes where genetic integrity may be compromised (Young *et al.* 1996).

4.2.2 Demonstrating the framework in the Tasmanian Midlands

To demonstrate PUCA, we used two restoration sites (Ross and Cressy) in the Tasmanian Midlands, Australia (Figure 4.2; see Appendix C1 for Cressy results). We first defined a target region that contained both the Ross and Cressy sites. While the region could be defined using state boundaries (Gray and Hamann 2011), ecoregions (Olson *et al.* 2001), or a specific geographic distance around the restoration site, we followed Whitten *et al.*'s (2011) approach of defining this region as a combination of parts of the Northern Midlands and South East bioregions (https://www.environment.gov.au/land/nrs/science/ibra) with similarities in geology, climate,

topology, and ecological features (hereafter the Midlands; Figure 4.2). We focused on six eucalypt species that are the dominants of the surrounding remnant woodlands - *Eucalyptus rodwayi*, *E. amygdalina*, *E. tenuiramis*, *E. ovata*, *E. viminalis* and *E. pauciflora* (Table 4.1) and constrained our study to the natural distribution of these species on the island of Tasmania (Appendix C2). Natural distribution records for each species were obtained from the Natural Values Atlas (https://www.naturalvaluesatlas.tas.gov.au/; accessed 2nd January 2015). Duplicate records and records within 100 m of another observation were removed.

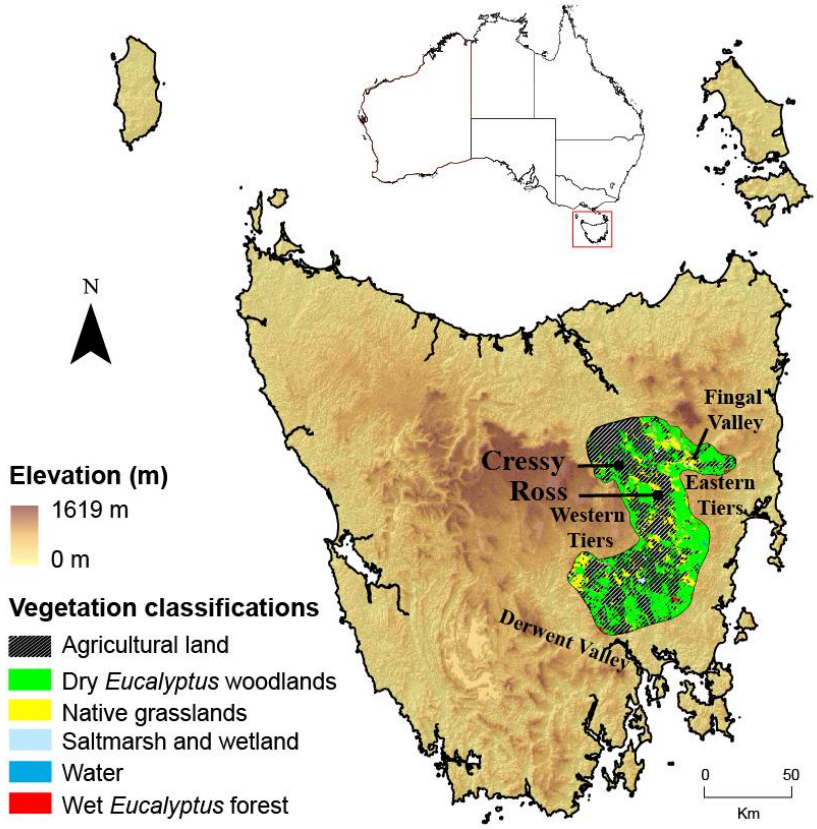

Figure 4.2. The Midlands restoration region (grey polygon) on the island of Tasmania, Australia, and the two restoration sites at Ross and Cressy (black squares), where current ecological restoration is aiming to restore biodiversity by recreating vegetated corridors among fragmented remnant forests between the Eastern and Western Tiers. The Midlands is arid by Tasmanian standards, with average summer maximum temperature ranging from 18 to 25 ˚C and average summer precipitation of 104–225 mm. Also overlain on the Midlands are the broadscale vegetation classification based on TASVEG, along with the complex topology of Tasmania derived from a 90 m Digital Elevation Model. Key geographic localities are labelled.

Table 4.1. The number of distribution records for the six dominant *Eucalyptus* species in the Midlands of Tasmania downloaded from the Natural Values Atlas (https://www.naturalvaluesatlas.tas.gov.au/; accessed 2 Jan 2015). Also shown are the species-level median altitude, minimum temperature of the coldest week (TMNCW), maximum temperature of the warmest week (TMXWW), and annual precipitation (RANN) for the three Tasmanian endemic (*Eucalyptus rodwayi*, *E. amygdalina*, and *E. tenuiramis*) and the three non-endemic (*E. ovata*, *E. viminalis*, and *E. pauciflora*) species used in the study. The natural geographic distribution of each species is shown in Appendix C2. Species have been separated by their subgenera (*Eucalyptus* and *Symphyomyrtus*).

Species	Distribution points	Altitude (m)	TMNCW (°C)	TMXWW (°C)	RANN (mm)
Subgenus *Eucalyptus*					
E. amygdalina	11,069	217	2.6	21.8	878
E. pauciflora	1,533	515	0.4	21.1	725
E. tenuiramis	1,803	245	2.7	21.4	752
Subgenus *Symphyomyrtus*					
E. ovata	3,208	150	3.1	21.9	786
E. rodwayi	1,143	585	0.4	20.2	857
E. viminalis	9005	237	2.3	21.7	839

The regional climate space of the Midlands was defined using the current (baseline) climate surfaces (1976-2005) obtained from ANUCLIM version 6.1 (Xu and Hutchinson 2012). Climate change grids for minimum and maximum temperature, rainfall, and evaporation were calculated relative to the ANUCLIM baseline, for three future periods representing 2010–2039, 2040–2069, and 2070–2099 (hereafter 2020s, 2050s, and 2080s, representing the mean values of the 30 year periods). Climate projections were calculated from a dynamically downscaled regional climate model (see Corney *et al.* 2010). We used six Global Circulation Models (GCMs) that were dynamically downscaled to ~10 km resolution by the Climate Futures for Tasmania project (ECHAM5/MPI-OM, CSIRO Mk 3.5, GFDL-CM2.0, UKMO HadCM 3, GFDL-CM2.1 and MIROC3.2 (medres)). These climate models represent the observed southeast Australian climate means and variability well (Smith and Chandler 2010), and cover a range of projected rainfall changes in southeast Australia (Christensen *et al.* 1996). ANUCLIM was used to interpolate each GCM to 1 km resolution and generate monthly mean data for 11 temperature and 8 precipitation bioclimatic variables (Appendix

C3), for the baseline and future periods. Results for the restoration sites are based on the A2 high emission scenario (IPCC 2013), which global emissions are currently tracking (Peters *et al*. 2013). To illustrate our framework, we aggregated the projected value made by the six GCMs for each grid cell to create a multi-model mean (MMM) for each bioclimatic variable for the 2020s, 2050s and 2080s. A MMM approach smooths out the annual and decadal variability and reveals the climate response independent of the different model configurations (Fordham *et al*. 2011).

We parameterised the PUCA model using a truncating buffer *w* of 5 km radius around the two restoration sites, and a 2-unit threshold on the dissimilarity scores to identify the most aligned candidate seed sources with each restoration site. We selected the 2-unit value as it accounted for over 90% of species records within a 15 km radius around the restoration site that occupied an analogous climate with the baseline truncated, regional climate space (data not shown), which is likely a conservative geographic definition of a local provenance for these species (e.g. Gauli *et al.* 2014). However, within PUCA there is the provision to automatically calculate this threshold using the mean dissimilarity scores for each species record within the truncation buffer. Candidate seed sources for baseline and future climates of the restoration site were then identified as species records occurring within or outside a fragmented landscape using an urban/agriculture polygon created from the vegetation classification layer TASVEG version 2 (Figure 4.2; Kitchener and Harris 2013).

4.3 Results

The spatial pattern of species records matching the baseline and projected 2020s climate conditions for the Ross and Cressy restoration sites was consistent with a local provenancing strategy, in that the majority of points occurred within 15 km of the restoration site (Figure 4.3; Appendix C1). By the 2050s, only distant populations of the six species were in analogous climates and by the 2080s none of the six species' distribution points were in climates considered analogous to the projected climate of Ross and Cressy (Figure 4.3; Appendix C1). While we have used the MMM of six GCMs to identify analogous climates, we were still able to identify similar areas for each species when using only extreme GCM projections (i.e. UKMO HadCM 3 [warmer maximum temperatures and increased annual precipitation; Appendix C4] and MIROC3.2 [warmer maximum temperatures and decreased annual precipitation; Appendix C4]; Appendix C5). However, the increased aridity projected by MIROC3.2 resulted in non-analogous conditions for all eucalypt species at Ross by the 2050s (Appendix C5).

The percentage of climatically matched species records occupying modified agricultural landscapes was variable, yet the pattern was consistent through time (with the exception of *E. rodwayi*; Figure 4.3). By the 2050s, there was a slight decrease in the percentage of matched records in modified landscapes, except for *E. tenuiramis*, which had a higher density of records in modified landscapes throughout the Derwent Valley (Figure 4.2; Figure 4.3).

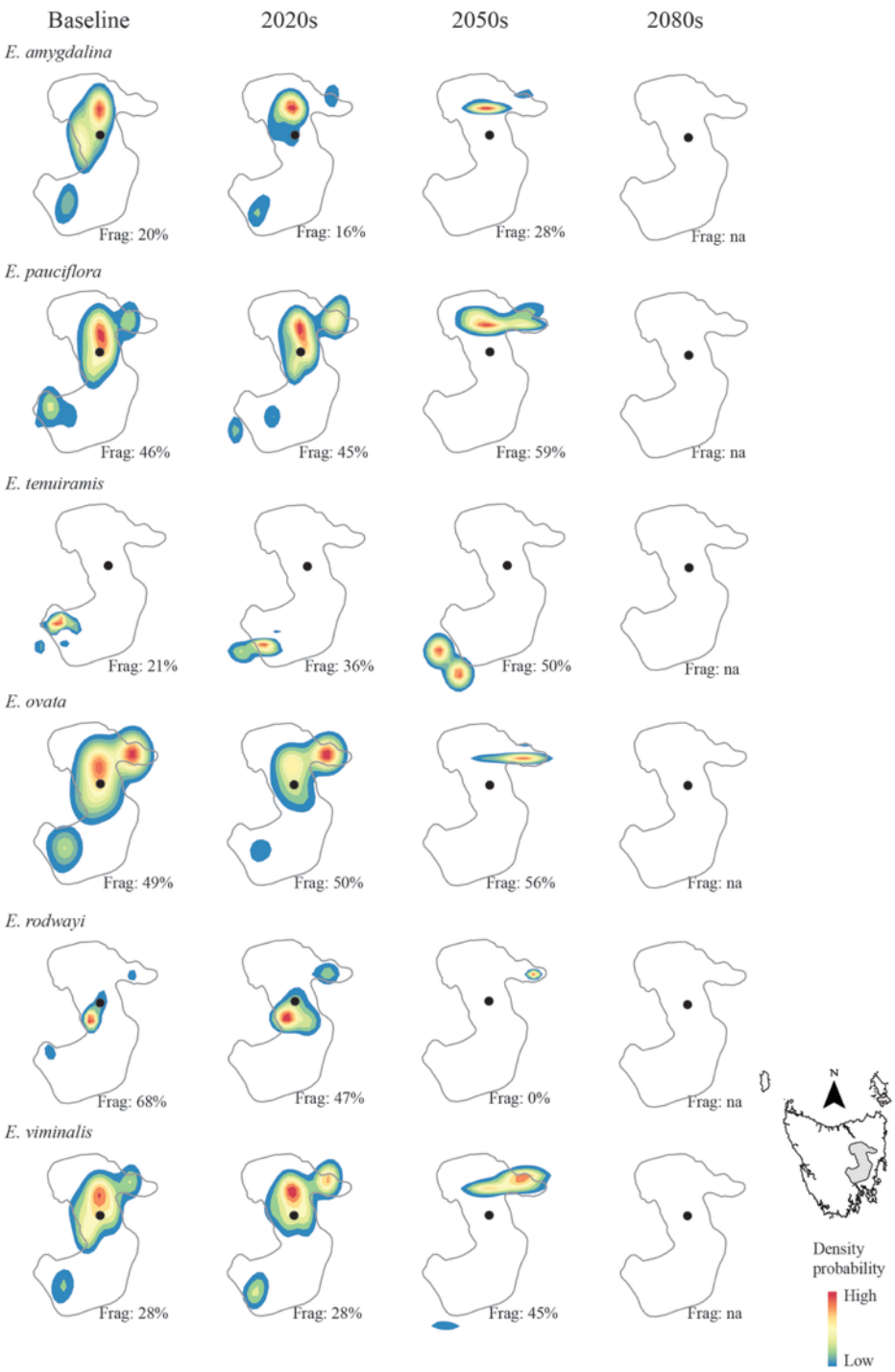

Figure 4.3. The density probability function and percentage of climatically matched records within modified landscapes (Frag) for three Tasmanian endemic (*Eucalyptus rodwayi*, *E. amygdalina*, and *E. tenuiramis*) and three non-endemic (*E. ovata*, *E. viminalis*, and *E. pauciflora*) species climatically analogous to the Ross restoration site (black dot) for the baseline climate (1976–2005) and the projected multi-model mean climates for the 2020s, 2050s, and 2080s under the A2 emission scenario. The colour ramp corresponds to the smoothed kernel density probability where hot colours (yellow to red) represent higher density of distribution points occurring in analogous climates projected for the restoration site. Maps for the Cressy restoration site are given in Appendix C1. While *E. tenuiramis* is not found at Ross and is predominantly a south-eastern species (Appendix C2), we identified distribution records in the Derwent Valley that currently occupy climates analogous to the baseline, 2020s, and 2050s climates of Ross.

4.4 Discussion

4.4.1 Assumptions of the operational framework

To implement the PUCA framework, several assumptions were necessary. For example, we assumed populations evolve locally adaptive traits in response to the macroclimate, which can be exploited to increase the climate-resilience of restoration plantings through time. Evidence for local adaptation is generally demonstrated by fitness differences among provenances grown in reciprocal transplant or common garden experiments (McLean *et al.* 2014), or correlative links between functional traits and environmental variables (Gauli *et al.* 2015). While we do not account for other selective factors such as soils (Wright 2007), we assume the macroclimate is one of the most important factors limiting the distribution of a species. Indeed, species are likely shaped by direct or indirect facets of the macroclimate (Thomas 2010; Aitken and Bemmels 2015) and, at least in *Eucalyptus*, there is evidence that distributions are likely to be predominantly shaped by temperature and precipitation (Davidson and Reid 1985; Brawner *et al.* 2013 and references within).

The PUCA framework also assumes that the different components of the macroclimate have equal weighting on the fitness of a species, and this weighting will be conserved into the future. This assumption may often be violated and species specific. Future improvements to the framework could include the differential weighting of climate variables based on results of provenance performance in field trials or functional trait correlations. For example, provenance variation in functional traits in *E. pauciflora* seedlings was predominantly associated with the home-site maximum temperature (Gauli *et al.* 2015), suggesting the up-weighting of principal component axes associated with extreme temperature. Another assumption is that plant responses to climate change are not altered by increased carbon dioxide concentrations ($[CO_2]$). Elevated atmospheric $[CO_2]$ are predicted to have beneficial effects on plant physiology and growth (Wang *et al*. 2012) and even reproduction (LaDeau and Clark 2001). However, novel interactions observed between elevated $[CO_2]$ and increasing

temperature under experimental conditions suggest responses may be species-specific (Wang *et al.* 2012; Lewis *et al.* 2013).

For demonstration purposes, we assume that a candidate seed source with a climate dissimilarity greater than 2-units from the baseline or projected climate of the restoration site will exhibit maladaptation. Scaling this threshold requires development of general transfer functions (O'Neill *et al.* 2008) and is a current research objective (Bailey *et al.* 2013). We have also tried to reduce the risk of sampling climatically matched seed sources which may have poor seed crops or exhibit inbreeding depression by flagging seed sources likely to be in fragmented landscapes. Reduced reproductive output, reduced outcrossing rates and increased inbreeding depression are often syndromes of fragmented and small populations (Young *et al*. 1996), including *Eucalyptus* (Borralho and Potts 1996; Mimura *et al.* 2009; Gauli *et al.* 2013). However, such effects may be species specific (Breed *et al.* 2013; Gauli *et al.* 2013) and dependent on pollinator mobility (Aguilar *et al.* 2006; Kramer *et al.* 2008). By accounting for these factors (e.g. by over-sowing), seed from fragmented landscapes may still be of value (Ottewell *et al.* 2009), particularly if there is no alternative.

4.4.2 Applying the framework for research and operation in the real world

The premise of the climate-adjusted provenancing (the underlying seed sourcing strategy of PUCA) is to mix local and climatically matched non-local gene pools to optimise the adaptive potential of the restoration plantings in the face of uncertain future climates (Prober *et al*. 2015). How much non-local seed should contribute to the mix will depend on a number of factors, including seed availability and quality (see above), potential maladaptation of candidate provenances of long-lived species during establishment as the projected climate is yet to materialise (Grady *et al.* 2015), and the relative uncertainty in future climate projections (i.e. Appendix C4). Although seed choice

will depend on the scale and scope of a restoration project, we propose three ways through which the PUCA output could be applied to guide seed mixing. For example, a researcher or practitioner may apply the results by:

(1) Targeting areas with seed sources that are consistently analogous to the restoration site across multiple future time periods and climate models. This approach is conceptually similar to that proposed by Gray and Hamann (2011) and may consist of using equal proportions of local and climatically matched non-local seed. For example, in the present study the Fingal Valley was consistently identified as an area with analogous future climate to the Ross restoration site for several species (Figure 4.3). Thus restoration plantings at Ross could include, for example, 50% local and 50% randomly sampled provenances from within the Fingal Valley.

(2) Using the uncertainty in the climate projections to derive an exponential decay curve to guide the sampling effort allocated to the different future time periods, where sampling would be either a uniform or random sample of the area of analogous climate. For the Midlands region, the 2050s and 2080s show the greatest model uncertainty (i.e. increased range in mean values; Figure S2). Thus the exponential decay curve derived for the Ross restoration site down-weights the contribution of seed sources climatically matched to the 2050s and 2080s compared to the 2020s (Figure 4.4), and suggests that nearly 30% of the seed mix should come from seed sources matched to the 2020s.

(3) Apply either (1), (2) or a combination, and bias provenance selection to minimise (or maximise depending on objective) the gene flow or genetic divergence between the local and non-local provenances. Thus, with approach (1) and the secondary consideration to minimise genetic divergence, provenances from the Fingal Valley would be selected over those from the more distal Derwent Valley. However, if the supplementation of genetic diversity in depauperate remnant stands is an objective (Broadhurst *et al*. 2008) the more distal area may be targeted.

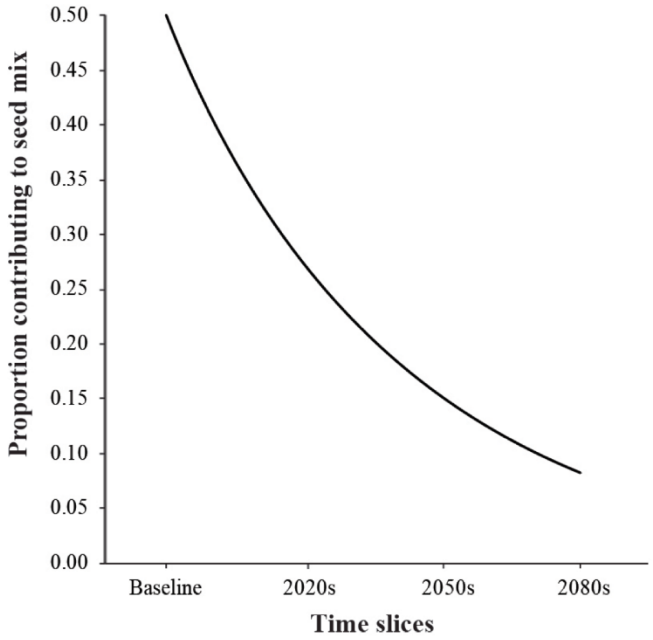

Figure 4.4. An example of using the uncertainty in the Global Circulation Models (GCMs) to estimate the proportion or sampling effort of candidate seed sources identified for baseline (1976-2005) and the projected climate for the 2020s, 2050s, 2080s. The curve is calculated as $y = 0.5 - \left(1/\sqrt{(\mathrm{GCM_{max}} - \mathrm{GCM_{min}})}\right)$, where 0.5 assumes 50% of the seed mix will be from local provenances, and $\mathrm{GCM_{min}}$ and $\mathrm{GCM_{max}}$ are the range of mean projected values for a bioclimatic variable. In this example, the curve has been calculated using the inverse of the square-root difference between the maximum and minimum of six GCMS for the annual precipitation projected for the 2020's, 2050s, and 2080s under the A2 emission scenario (Appendix C4). For example, a mix could include 50% from baseline climates, 25% from 2020, 15% from 2050, and 10% from 2080.

Decisions about where and how much to sample will need to consider the ecological and genetic implications of moving genotypes around the landscape (Bucharova 2016). These can include (1) the potential for inter- and intra-specific hybridisation through pollen dispersal which could lead to heterosis (superiority of hybrid over pure stock) (Costa e Silva *et al.* 2014), outbreeding depression caused by disruption of locally adapted gene combinations (Costa e Silva *et al.* 2012), or off-site genetic contamination (Potts *et al.* 2003); and (2) the spread of wildings, weeds, diseases or pathogens (Ricciardi and Simberloff 2009). Depending upon scale, translocations may also have extended impacts on dependent organisms (Whitham *et al.* 2006; Sinclair *et al.* 2015). Byrne *et al.* (2011) and Weeks *et al.* (2011) provide decision trees to evaluate the likelihood of ecological and genetic risks to the surrounding native remnants. For example, following these decision trees, there is a 'low risk' of potential ecological and genetic disruption to the surrounding native remnants by using non-local provenances of *E. pauciflora* at Ross. This is because the site is within the natural distribution of *E. pauciflora* (Appendix C2), the species exhibits low neutral genetic divergence in Tasmania (Gauli *et al.* 2014), and its flowering time overlaps little with the related cross-compatible species in the area (Williams and Potts 1996).

4.4.3 Future research needs

PUCA provides researchers and practitioners a tool to identify non-local seed sources which may be best suited to future climates for ecological restoration or reforestation. However, empirical evidence demonstrating the benefits of mixing local with non-local provenances is generally lacking (Bucharova 2016). By increasing the wider adoption of common garden experiments embedded in restoration plantings (e.g. Bailey *et al.* 2013; Gellie *et al.* 2016) using seed from local and non-local provenances identified by PUCA, further development of four core areas of research may proceed: (1) refinement of the assumptions made by PUCA (see above), (2) impact of other environmental surfaces (e.g. soil), (3) examination of the direct and indirect effects non-local genotypes may have on the local ecology (Bucharova 2016), and (4) extended applications of PUCA including the identification of potential areas of a species distribution that may be important to conserve for *in situ* climate-resilience of species or flora in general.

Acknowledgements

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Chapter 5: Provenance and seed mass determines the seed germination success of *Eucalyptus ovata* (Myrtaceae)

Abstract

Eucalyptus ovata is a medium size tree which grows from near sea level to sub-alpine regions in the south-east of Australia and is increasingly being used for woodland restoration in Tasmania. Given the wide altitudinal range of the species, we investigated whether a wet, cold stratification treatment enhanced seed germination of high altitude provenances. Open-pollinated seeds were harvested from five trees from a high and low altitude provenance within each of the five geographic regions from across *E. ovata*'s distribution in Tasmania. Chilling imbibed seeds at 5 °C for three weeks had no effect on the overall proportion of viable seed which germinated. There were, however, significant provenance differences in seed weight and the germination traits (i.e. proportion of viable seed, germination rate and overall proportion germinated) which were variably linked to differences in altitude. Seed viability tended to increase with seed mass and provenance-level correlations amongst germination traits suggested that seeds from different provenances differed in germination vigour. These results indicate that provenance rather than a pre-treatment determines germination success of *E. ovata* seed, but these provenance differences are not predictable and that selection of heavier seeds may increase germination success in the nursery and in direct seeding applications.

5.1 Experimental and Discussion

Eucalyptus ovata Labill. (swamp gum) is one of the most widely distributed eucalypt species on the island of Tasmania, Australia, where it occurs from near sea level to subalpine regions with altitudes of just over 800m a.s.l. (Williams and Potts 1996). It is a medium to tall tree which is often found in grassy woodlands that are subject to periodic flooding (Williams and Potts 1996). Many of the forests and woodlands occupied by this species are currently listed as threatened community

types under state law (i.e. *National Conservation Act* 2002) due to extensive clearing for agriculture (Kirkpatrick *et al.* 1988; Fensham 1989) and current landscape-scale restoration projects are using diverse wild seed collections of *E. ovata* to develop plantings which link and buffer existing fragmented vegetation.

With an increased interest in large-scale seed germination for nursery or direct seeding purposes there is a need to better understand the germination characteristics of *E. ovata*. Separate studies on single lowland populations of *E. ovata* in Tasmania, Australia, found high germination performance without applying a pre-treatment (Boland *et al.* 1980; Wood 2012). However, the germination response may vary between provenances of the same species due to genetic or environmental factors (Humara 2000; Bischoff *et al.* 2006; Rix *et al.* 2012). For example, higher altitude provenances of *E. regnans, E. delegatensis* and *E. pauciflora* (which are generally exposed to cooler temperatures) showed enhanced germination performance after a wet, cold stratification treatment (Beardsell and Mullet 1984; Close and Wilson 2002). In the present study we tested the hypothesis that seeds from high altitude provenances of *E. ovata* have a greater stratification requirement for germination than those from low altitude provenances. We sampled both high and low altitude provenances from five geographic regions (Table 5.1) which covered the known range of *E. ovata* in eastern Tasmania, and west coast populations with affinities to *E. ovata* (Williams and Potts 1996). Five trees (seed lots) from each provenance were sampled at least 100 m apart, with approximately 500 g of open-pollinated capsules collected. Capsules were then air-dried, seeds extracted from the dried capsules, and stored in air tight zip-lock bags in the dark at 5 °C.

Table 5.1. Location and 50 year climate averages for the ten provenances used in the current study. Provenances were assigned to five geographic regions in Tasmania and defined as high or low altitude provenance based on their elevation above sea level (m. a.s.l.). Long-term climate variables are the average of 50 year daily observations which were calculated from interpolated daily weather station data (Jeffrey *et al.* 2001).

Provenance	Region	Longitude (°)	Latitude (°)	Altitude (m a.s.l)	Precipitation (mm)	Minimum temperature (°C)	Maximum temperature (°C)	Frost days[A]	Heat days[B]
Scotts Peak	South East	146.3807	-42.9005	327	1732	-2.8	32.8	24	4
Garden Island Creek	South East	147.1526	-43.2397	11	846	-0.5	34.3	3	4
Lake Leake	East	147.7958	-42.0117	614	889	-5.9	30.0	72	1
Asplawn	East	148.2293	-41.9405	10	702	-0.6	33.9	4	3
Nunamara	North East	147.2721	-41.3684	428	1095	-3.5	30.5	35	2
Pipers Brook	North East	147.2365	-41.0595	64	804	-0.6	29.9	4	1
Woods Lake	Central	147.0275	-42.0760	742	706	-6.9	30.5	99	1
Connorville	Central	147.1339	-41.8888	280	657	-5.7	33.4	53	6
Lake Burbury	West	145.6873	-42.0889	262	2523	-2.5	32.4	16	4
Henty River	West	145.2676	-42.0273	11	1565	-0.6	32.5	4	3

[A] Frost days were calculated as the sum of days within a given year where the minimum daily temperature was below 0 °C then averaged over 50 years.
[B] Heat days were calculated as the sum of days within a given year where the maximum daily temperature was equal to and above 30 °C then averaged over 50 years.

Eighty fully-ripened seed (i.e. swollen seed with an intact black testa) were randomly selected from each seed lot. Seeds were then divided into four subsamples of 20 seeds and weighed. Two subsamples were randomly allocated to the wet, cold stratification treatment and imbibed on 1% agar in 90 mm-diameter Petri dishes for three weeks in the dark at 5 °C (fluctuated between 4.5 and 6.5 °C). The remaining two subsamples were allocated to the control treatment and were imbibed in Petri dishes with 1% agar a day prior to the commencement of the experiment. The germination experiment was undertaken using two replicates, each comprising the various combinations of pre-treatment (n = 2 [control and stratified]) and seed lot (n = 50 [five seedlots by 10 provenances]) which were represented by one Petri dish (each replicate comprised n = 100 Petri dishes) stacked on a single shelf of a temperature controlled incubator set at 20 °C with an 8-hour light / 16-hour dark photoperiod (i.e. optimal germination conditions as reported in Wood 2012). Within each replicate, Petri dishes were randomised into a row/column experimental design comprising five incomplete blocks of four rows and five columns. This design was generated using CycDesigN version 4.0 (VSN International Ltd., Hempstead, UK).

Germination counts were taken after 2, 5, 7, 9 and 18 days. Seeds with a protruding radicle at least 1 mm long and with unfolded cotyledons were considered germinated and normal (Boland *et al.* 1980), and were counted and removed. At the end of the experiment, seeds which failed to germinate were checked for viability by squashing the seed with a pair of forceps (Boland *et al.* 1980). Seed with a firm white embryo were considered as viable ungerminated seed, otherwise seed was considered inviable if hollow or the embryo was decayed and soft.

The effect of the stratification treatment on the germination characteristics of *E. ovata* were summarised by three response traits: (i) seed viability (the proportion of total seeds sown which were viable), (ii) germination rate (estimated from the proportion of seeds that had germinated by day-2 in the stratified treatment), and (iii) total seed germinated (the proportion of viable seeds which

germinated by the end of the experiment). Generalised linear mixed models were fitted to each response trait using PROC GLIMMIX (SAS Version 9.2, SAS Institute, Cary, USA) and the number of seeds germinated (events) out of the total (trials) for each Petri dish, assuming a binomial distribution of errors and a logit link function. Preliminary models found the fixed effect of position and the random effect of replicate within position did not significantly affect the germination traits (data not shown) and were subsequently removed from the final models. For each model, seed mass was fitted as a covariate and stratification treatment, provenance altitude, region, and their interactions fitted as fixed effects; seed lot within provenance (i.e. nested within altitude by region) was fitted as a random term in all models except when modelling the proportion of viable seed germinated due to the model failing to converge. A model with a normal link function was also fitted to test for provenance effects on seed mass itself. In this case altitude, region and their interaction were fixed effects; and the family nested within provenances was a random term.

Despite considering the provenance of *E. ovata* seeds from a wide range of altitudes, we were unable to find any evidence for cold, wet stratification enhancing germination success. Stratified seeds germinated earlier than unstratified seeds, no doubt due to its more advanced stage of imbibition. On day-2, 52% of stratified seeds had germinated compared with 1.5% of unstratified seeds. However, this difference was lost by day-5 (70% of the stratified seeds had germinated compared with 68% of the unstratified seeds). At the final count, 79.9% of the seed was viable (mean stratified = 79.8%, control = 80.0%) and 7.4% of this viable seed remained ungerminated (stratified = 7.6%, control = 7.2%). There was no significant main or interaction effect involving stratification on either trait (seed viability $F_{(1,135)} = 2.23$ $P > 0.05$; total seed germinated $F_{(1,179)} = 0.00$ $P > 0.05$), and the percentage of viable ungerminated seed was below the 20% threshold expected if primary dormancy was present (Boland *et al.* 1980). The absence of a stratification requirement for the high altitude provenances of *E. ovata* contrasts with other studies of high altitude provenances of *Eucalyptus* (Boland *et al.* 1980; Beardsell and Mullett 1984; Close and Wilson 2002), and other tree

species (reviewed by Moncur *et al.* 1997 and Bell 1999), which often show enhanced germination after stratification.

While overall germination was high, the proportion of viable seeds that germinated (mean = 71.6%) was lower than the 100% previously reported for a low altitude provenance of *E. ovata* (Wood, 2012). This difference may be due to provenance variation within the species as we detected significant provenance differences in all germination traits and seed mass (i.e. significant region by altitude interaction and main effects; Figure 5.1). Such differences are commonly observed in multi-provenance studies (reviewed in Roach and Wulff 1987), including on *Eucalyptus* (*E. nitens*, Humara 2000; *E. delegatensis*, Battaglia 1993; *E. viminalis*, Ladiges 1974; *E. globulus*, Lopez *et al.* 2003), and may be due to genetic or maternal environment differences (Roach and Wulff 1987; Rix *et al.* 2012, 2015).

At the provenance-level, trait means were significantly correlated, indicative of general differences in germination vigour. For example, provenances with higher levels of viable seeds tended to have a higher proportion of viable seeds which germinated (n = 10; r = 0.78, P = 0.008). These traits were correlated with seed mass, such that provenances with heavier seeds tended to have greater viability (r = 0.62, P = 0.05) and a higher proportion of viable seeds which germinated (r = 0.71, P = 0.02). While there was a trend for provenances with faster germination to have a higher proportion of viable seeds germinated (r = 0.63, P = 0.05), provenance germination rate was not correlated with seed viability (r = 0.15, P = 0.68) or seed mass (r = 0.39, P = 0.27). Seed mass is a commonly studied seed trait which is under maternal control and can influence germination characteristics and even cause carry-over effects on later growth habits (Roach and Wulff 1987; Lopez *et al.* 2003). Nevertheless, when seed mass was fitted as a covariate in the binomial models, the provenance differences in germination traits were still significant (Figure 5.1).

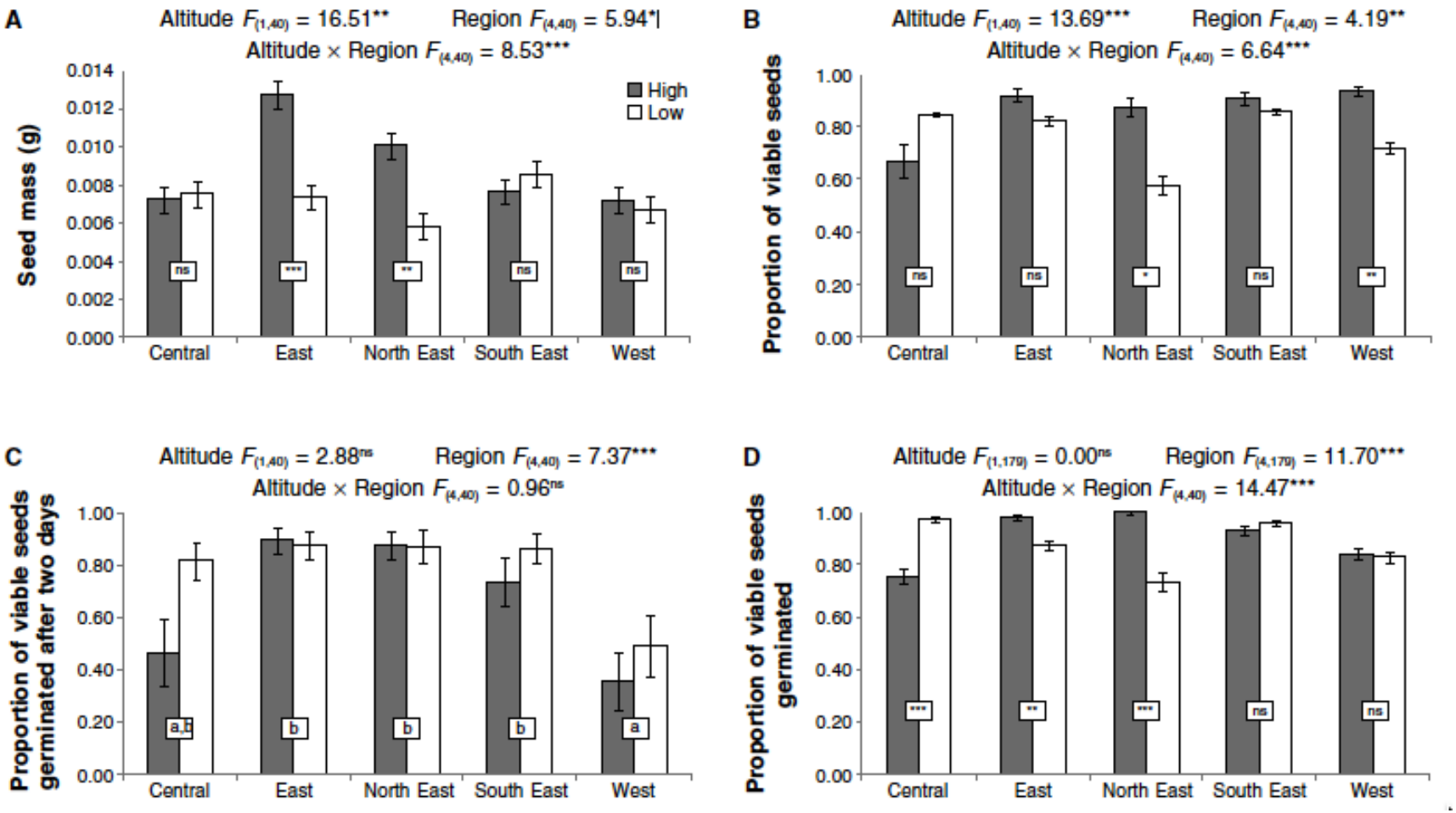

Figure 5.1. The least square means (± SE) for provenance effects (region by altitude interaction) on **A** seed mass, **B** proportion of viable seeds sown, **C** proportion of total germinated seeds in the stratification treatment by day-2, **D** proportion of total viable seeds which germinated by the end of the experiment. The results of the main and interaction effects from the generalised mixed models for each germination trait are shown above each bar graph. The results from a Tukey-Kramer multiple comparison test for altitude differences in each region are shown superimposed over the columns (ns = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Letters in **C** denote significant differences between the main effect of region using a Tukey-Kramer multiple comparisons test. Grey bars correspond to high altitude provenances and white bars correspond to low altitude provenances (Table 5.1). The pooled SE of the estimated means were approximated by the delta method using the *ilink* function in PROC GLIMMIX (SAS Version 9.2, SAS Institute, Cary, USA).

Some provenance differences in seed mass and germination traits did appear to be related to home-site altitude, but the altitude effect was not consistent (Figure 5.1). For example, seed mass differences between provenances were only significant in two regions (East and North-East) and in both cases this involved an increase in seed mass in the high altitude population (Figure 5.1). Provenance-level variation in seed mass may be related to the level of resource allocation by the maternal tree (i.e. environmental maternal effects; Roach and Wulff 1987), however, the relationship between seed mass and altitude seems to be a species-specific response with positive (Pluess *et al.* 2005; Moles and Westoby 2006) and negative (Baker 1972; Bu *et al.* 2007; Guo *et al.* 2010) relationships reported.

Together, these results indicate that germination of *E. ovata* seed varies among provenances, but there is not a general altitude effect or a requirement for cold, wet stratification in higher altitude provenances. The effect of seed mass on the germination traits studied suggest that germination in the nursery or by direct seeding could be enhanced by selecting heavier seeds, which might lead to more viable seed being sown and hence a greater proportion of seeds germinating.

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Chapter 6: Using signals of selection in functional traits to model spatiotemporal change in the selection surface

Abstract

Understanding the contemporary patterns of adaptive variation within forest tree species is fundamental for the testing and implementation of assisted gene flow strategies for restoration purposes, such as climate-adjusted provenancing. As common garden field trials are often costly to establish and can take many years for local adaptations to emerge, especially for long-lived species such as forest trees, we here develop a novel approach using quantitative genetics and glasshouse studies of seedling functional traits to 'fast track' the detection of climate adaptations in untested species. Our approach involved firstly applying a 'filter' to only retain functional traits that show (i) significant between-provenance variation, (ii) signals of putative divergent selection (i.e. significant $Q_{ST} > F_{ST}$ comparison), and (iii) quantitative genetic independence. The second stage then takes the remaining functional traits to derive a climatically-aligned 'adaptively-enriched genetic space' that is used to produce a 'climate selection surface' that is predicted to have historically shaped the adaptive variation in functional traits at the provenance level. We demonstrate this novel approach using seedlings grown in a glasshouse from 312 open-pollinated families collected from 45 provenances of the woodland species *Eucalyptus ovata* in Tasmania, Australia. Provenance variation in putatively adaptive functional traits was significantly associated with two othogonal climate gradients that were used to predict and forecast spatial changes in the climate selection surfaces for contemporary and future climates, respectively. Translating changes in multiple climate variables into biological effects on fitness is problematic, and the current approach is one of the first attempts to develop models of future climate change impacts by weighting climate variables in a manner relevant to the biological system under study.

6.1 Introduction

Since the emergence of industrial-era climate change, global mean average temperatures have increased by 0.85˚C and are projected to continue rising by up to 4˚C over the next 100 years (IPCC 2014). Incorporating current and future climate change into the management of natural resources has become increasingly important in conservation ecology (Heller and Zavaleta 2009; Lawler 2009; Jones *et al.* 2016). A leading strategy to minimise the loss of biodiversity under climate change is to translocate populations and species from maladaptive habitats to predicted habitats that promote the short and long-term persistence of the species (Aitken and Whitlock 2013). The concepts of assisted gene flow within (assisted migration) or outside (assisted colonisation) the species range has gained increased popularity among conservation scientists as an adaptive strategy to climate change (Thomas 2011; Lunt *et al.* 2013). Assisted gene flow attempts to increase the frequency of climate-adapted genotypes in a population to promote adaptation over consecutive generations (Aitken and Whitlock 2013). While there are unpredictable and potentially important flow-on effects with these strategies (Ricciardi and Simberloff 2009; Bucharova et al 2016), a key practical aspect of assisted gene flow is the ability of the translocated population/species to establish successfully in the new habitat (Gray and Hamman 2011; Grady *et al.* 2015).

The recently proposed climate-adjusted provenancing strategy (Prober *et al.* 2015) is a special case of assisted gene flow, and has gained increased interest among ecological restoration and reforestation practitioners. The premise of this strategy is to maintain a local provenancing strategy (Mortlock 2000; McKay *et al.* 2005), but supplement the local germplasm with seed from non-local provenances selected along a spatiotemporal gradient of environmental change. The climate-adjusted provenancing strategy (and assisted gene flow strategies in general - Aitken and Whitlock 2013) fundamentally depends on the exploitation of inherent pre-existing differences among provenances

in their adaptation to climate. This requirement assumes the macroclimate has been a major agent in shaping the adaptive landscape of a species in recent evolutionary time.

There are multiple ways in which to experimentally detect local adaptations to environmental pressures, and the 'gold-standard' remains the establishment of reciprocal transplant common-garden field trials (Kawecki and Ebert 2004; Blanquart *et al.* 2013). Indeed, there is a long history of provenance testing in widespread forest tree species planted along elevation and climate gradients (Aitken and Bemmels 2015), which have been retrospectively used to study and demonstrate local adaptation to the macroclimate (Matyas 1994, 1996; Rehfeldt *et al.* 1999; Hereford 2009; Wang *et al.* 2010; Gray *et al.* 2016). Another approach to detect local adaptation is to study signals of selection in functional traits using the quantitative coefficient of population differentiation (Q_{ST}). Q_{ST} is a measure of quantitative genetic variation in a trait due to among population differences, which is analogous to the molecular coefficient of population differentiation (F_{ST}) (Whitlock 2008). The comparison of Q_{ST} to F_{ST} measured using putatively neutral molecular markers provides a test for whether a trait has evolved neutrally or through genetic drift (i.e. additive traits, $Q_{ST} = F_{ST}$), evolved through canalization (i.e. uniform selection, $Q_{ST} < F_{ST}$), or evolved through divergent selection ($Q_{ST} > F_{ST}$) (Whitlock 2008; Lamy *et al.* 2012). Signals of selection (i.e. $Q_{ST} > F_{ST}$) combined with correlative analyses of functional traits against components of the home-site (i.e. site from where the provenance originates) climate have allowed the detection of (i) traits mediating local adaptation, and (ii) the positing of the underlying selective agent likely to be driving the trait evolution (e.g. Gauli *et al.* 2015).

Identifying the key selective agents shaping local adaptations is important since it offers a way to construct effective management plans to mitigate potential impacts of future climate change. There is little doubt that locally adaptive traits have evolved in response to a suite of aboveground

(i.e. O'Reilly-Wapstra *et al.* 2004; McLean *et al.* 2014) and belowground (e.g. Macel *et al.* 2007; Johnson *et al.* 2010) selection pressures, which have been well demonstrated in a variety of different plant life forms (Leimu and Fischer 2008, Hereford 2009). The increased use of genome-wide association studies using significant outlying makers (Bragg *et al.* 2015) along with classic quantitative genetic studies (see above) are beginning to show an emerging suite of important climate variables that shape adaptive responses. Indeed, genetic (quantitative and molecular) variation among populations appears to be strongly associated with temperature (growing degree days, mean annual temperature, maximum summer temperature, minimum winter temperatures) and aridity gradients (Rehfeldt *et al.* 1999, 2002; De Kort *et al.* 2014; Steane *et al.* 2014; Gauli *et al.* 2015; Gray *et al.* 2016; Liepe *et al.* 2016).

While most of our understanding of local adaptation to the macroclimate in forest tree species comes from long-term common garden field trials, there is now an increasing need to 'fast track' the identification of key climatic factors for proactive conservation strategies (such as assisted gene flow). This need was recognised by Steane *et al.* (2014) using molecular markers, and we here provide a complementary strategy using signals of selection in seedling functional traits. We focused on the seedling stage of the regeneration cycle as it is a critical point in a plants life history that is exposed to enormous biotic and abiotic selection pressures (Kitajima and Fenner 2000; Moles and Leishman 2008; Bailey *et al.* 2012). Our conceptual framework consists of two stages (Figure 6.1). The first stage filters morphological traits using multiple criteria to identify a suite of genetically independent traits demonstrating highly significant signals of divergent selection. The second stage then defines an adaptively-enriched genetic space using the traits under divergent selection. This genetic space is then climatically aligned, and the independent climatic indices which are strongly associated with the adaptive genetic variation among provenances are spatially mapped to visualise the climatic selection surface. We demonstrate the application of this strategy using the woodland

dominant *Eucalyptus ovata* Labill. (black swamp gum), which is a target species used in ecological restoration projects in Tasmania, Australia. While undertaking this study, we (i) visualise the predicted changes in the selective surface under future climate projections, and (ii) test whether differential climate adaptation impacts early establishment success of planted seedlings following the translocation of provenances from diverse home-site climates into a restoration planting.

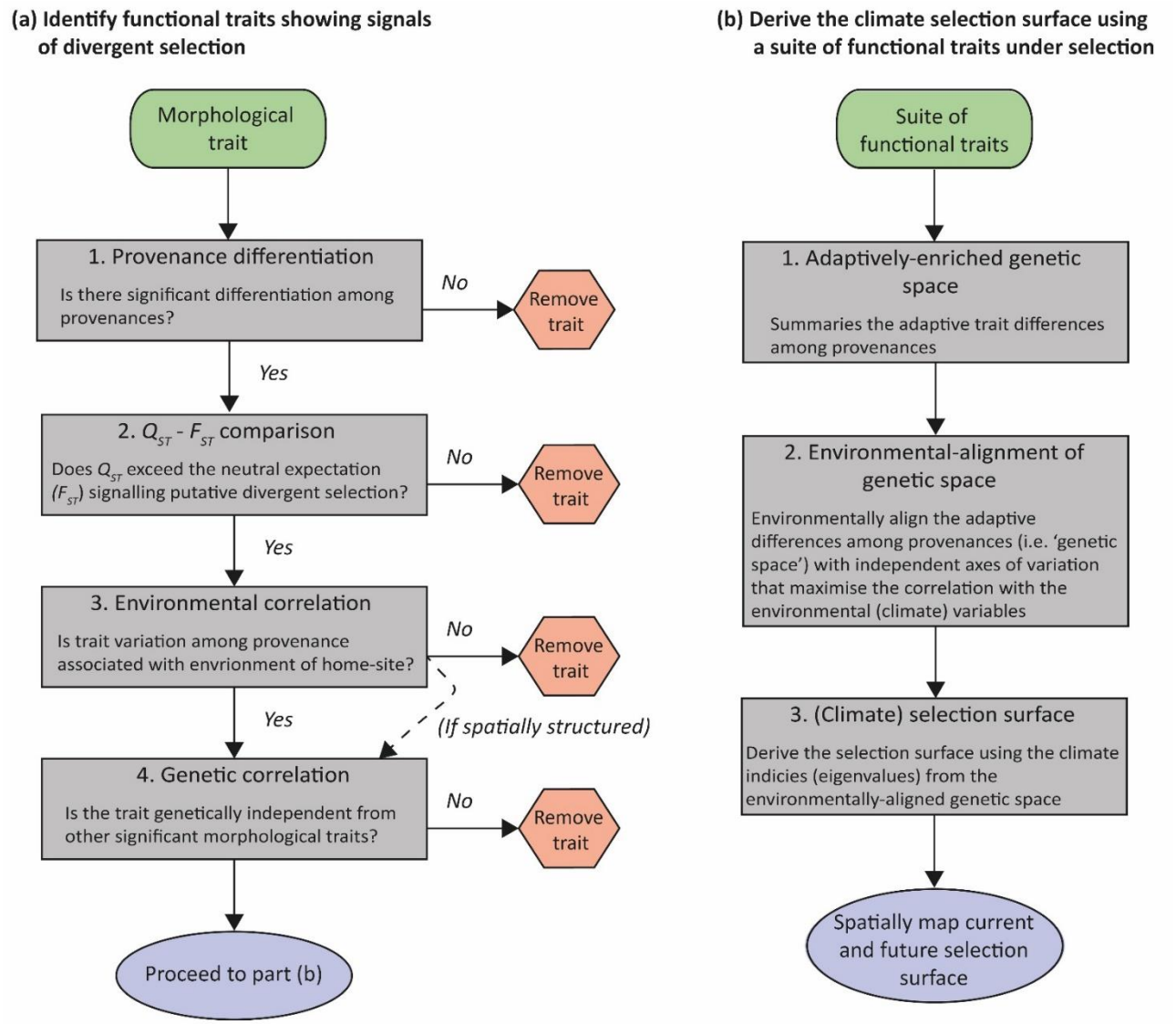


Figure 6.1. Conceptual approach to identify a climate selection surface for guiding provenancing strategies. This approach firstly identifies the quantitative traits showing signals of divergent selection (a) and then identifies the climate indices showing the maximum correlation with provenance variation in this adaptively-enriched multivariate genetic space (b). The selection surface is then spatially mapped using contemporary and future representations of the environmental variables to visualise the predicted optimal adaptive phenotype across the distribution of a species. The result section of this thesis has been ordered according to the logical flow of this framework.

6.2 Material and Methods

6.2.1 Study species and genetic material

Eucalyptus ovata is a widespread species found across south-eastern Australia, growing as a medium to tall tree on poorly drained soils (Nicolle 2006a). The current study focuses on the natural distribution of *E. ovata* on the island of Tasmania (Figure 6.2), where it is an important component of the biodiverse yet threatened sedgy-grassy woodlands (*Nature Conservation Act* 2002), and is a key species for on-going ecological restoration programs. The island of Tasmania is the southern-most extent of *E. ovata*, where it has one of the widest natural distributions among eucalypts across a topographically heterogeneous landscape. There is a strong east to west precipitation gradient across this distribution, with eastern populations (hereafter called provenances) receiving less than 500 mm annually compared to western provenances that receive upwards of 2000 mm annually. As the provenances in the north-western gene pool of *E. ovata* (western gene pool) are disjunct from the more continuous eastern gene pool (Figure 6.2) and their morphological affinities are unclear (P. A. Harrison, R. E. Vaillancourt, B. M. Potts unpublished data), we constrained our study to the more-or-less continuous core of *E. ovata* in eastern Tasmania (hereafter called eastern gene pool).

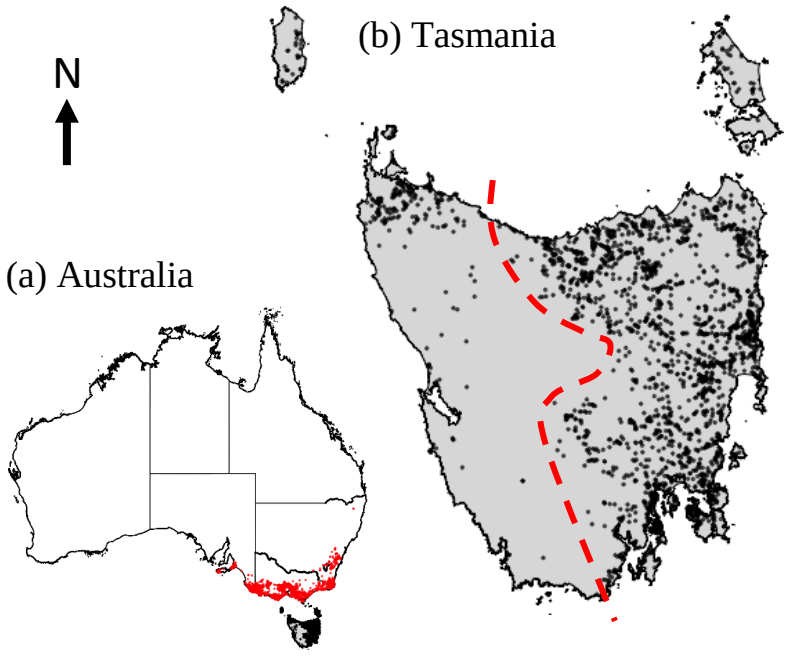


Figure 6.2. Distribution of *Eucalyptus ovata* in Australia (a) and Tasmania (b), where red points correspond to the mainland distribution from the Atlas of Living Australia (accessed 8th August 2014) and the black points correspond to the Tasmanian distribution from the Natural Values Atlas (accessed 18th April 2017). The red-dashed line shows the separation of the continuous 'eastern' and disjunct 'western' gene-pool of *E. ovata* in Tasmania.

To study genetic variation in *E. ovata*, we selected 45 provenances across both climate and altitudinal gradients that transect the eastern gene pool of *E. ovata* in Tasmania (Table 6.1). At each provenance, open-pollinated seed was collected from 5 to 11 trees sampled at least 100 m apart to reduce the probability of collecting from closely related individuals (Skabo *et al.* 1998). Each sampled tree was given a unique alphanumeric identifier and geographic (latitude and longitudinal) coordinates recorded using a Garmin GPSMAPS 64s GPS unit. The tree-level geographic coordinates along with altitude (extracted from an Australian bathymetric and topographic grid (Geoscience Australia; http://www.ga.gov.au) were used to calculate 27 temperature, precipitation, and radiation bioclimatic variables using ANUClim version 6.1 (Xu and Hutchinson 2012) (Appendix D1). The bioclimatic variables represent the 'current' climate and were the mean of the 1976-2005 period centred on 1990 (Xu and Hutchinson 2012). The tree-level altitude and bioclimatic variables were aggregated to provenance-level means for use in later analyses. Seed collections were maintained at the individual tree-level, hereafter termed 'family'. While the wide altitudinal range of *E. ovata* may argue for the presence of a seed dormancy breaking requirement (Beardsell and Mullett 1984; Close and Wilson 2002), the lack of a statistically significant increase in the rate of germination after a wet, cold stratification treatment suggested the absence of such dormancy in *E. ovata* (Chapter 5; Harrison *et al.* 2014). Thus, open-pollinated families were germinated in germination trays (randomised in respect to family) and placed in a germination house in separate batches of 60 randomly selected families during September to October 2013 at the commercial nursery (Woodlea nursery).

Table 6.1. Forty-five sampled *Eucalyptus ovata* provenances in Tasmania, Australia. Shown are the provenance name and code, the geographic coordinates of the site (latitude and longitude), the home-site altitude (m above sea level), mean annual temperature (TANN, ˚C) and mean annual precipitation (RANN, mm), and the number of open-pollinated families (individual trees) sampled at each provenance.

Provenance	Code	Latitude	Longitude	Altitude (m)	Families	TANN (°C)	RANN (mm)
Andover	AND	-42.3115	147.4914	401	6	10.4	545
Apslawn	APS	-41.9406	148.2320	7	8	13.3	664
Avoca	AVO	-41.8156	147.7538	204	9	11.6	510
Bignells Bothwell	BIG	-42.4029	147.1030	467	7	9.4	558
Brushy Lagoon	BL	-41.3909	146.7305	296	10	10.9	1015
Bust me Gall	BMG	-42.6062	147.6237	341	6	10.9	712
Coal Marsh	CM	-41.7573	148.1104	570	8	9.2	896
Conara	CON	-41.8311	147.4396	213	2	11.5	543
Connorville dam	CON1	-41.8866	147.1347	271	10	11.5	641
Connorville paddock	CON2	-41.8196	147.1106	177	8	11.0	617
Curringa	CUR	-42.5685	146.7717	93	6	11.6	562
Don	DON	-41.1733	146.3273	29	8	12.5	894
Doctors Rocks	DR	-41.0102	145.7725	18	5	12.4	965
Epping Forest	EF	-41.7633	147.3062	202	6	11.5	587
Ellesmere	ELL	-42.4080	147.2909	459	8	9.9	553
Fosterville	FOS	-41.9580	147.4305	199	11	11.3	505
Goulds Country	GC	-41.2151	148.1569	136	6	12.7	1011
Garden Island Creek	GIC	-43.2399	147.1541	15	7	12.0	814
Grove	GRO	-42.9866	147.1044	111	7	11.4	813
Ida Bay	IDA	-43.4429	146.9037	34	8	11.5	1152
Lake Leake	LL	-42.0107	147.7950	584	7	8.8	757
Little Swanport	LS	-42.3051	147.9642	33	7	12.7	551
Mount Cameron	MC	-40.9568	147.8158	45	7	13.3	769
Meander	MEA	-41.7028	146.5954	417	5	9.9	1049
Moogara	MOO	-42.7938	146.9470	182	6	11.2	705
Nunamara	NUN	-41.3687	147.2706	427	7	10.4	1077
Osterley	OST	-42.3358	146.7445	390	7	10.1	665
Pipers Brook	PIP	-41.0577	147.2366	44	6	13.0	777
Quorn	QUO	-41.9370	147.5691	274	4	10.9	526
Ross hills	ROSS1	-42.0417	147.6195	405	7	10.2	566
Ross lowlands	ROSS2	-41.9917	147.5556	239	5	11.3	507
South Arm	SA	-42.9962	147.4835	10	8	12.7	569
Scotts Peak Dam	SPD	-42.8993	146.3793	329	6	10.0	1713
Saltwater River	SR	-43.0287	147.7255	12	9	12.6	657
Stoner	STO	-42.4263	147.4395	457	7	10.0	610
Tea Tree	TEA	-42.6649	147.3729	148	6	11.7	536
Tolmans Hill	TH	-42.9162	147.3157	258	8	11.4	756
Tooms Lake	TL	-42.2131	147.7838	475	6	9.9	551

Continued from page 114

Provenance	Code	Latitude	Longitude	Altitude (m)	Families	TANN (°C)	RANN (mm)
Tyne River	TR	-41.4712	147.8243	303	6	11.1	861
The Thumbs	TT	-42.5888	147.8003	71	8	12.4	617
Tunbridge	TUN	-42.1368	147.4020	213	8	11.3	451
Uralla	URA	-42.5515	146.8561	166	5	11.3	521
Wayatina	WAY	-42.3932	146.5249	268	7	10.4	1036
Woods Lake	WL	-42.0772	147.0285	748	5	8.2	688
West Oatlands	WO	-42.2693	147.2985	445	7	9.9	513
			Mean	249	7	11.1	724

6.2.2 Genetic variation in seedling morphology

6.2.2.1 Glasshouse experimental design

A progeny trial was established in a common environment glasshouse at the University of Tasmania to investigate the genetic variation in seedling morphology among the 45 provenances of *E. ovata* sampled across the eastern gene pool in Tasmania. Three germinants from each family (*n* = 892 open-pollinated seedlings from 312 families) were potted into individual forestry propagation tubes (120 mm x 50 mm) three weeks after germination at the commercial nursery, and labelled with their unique family identifier. A randomised incomplete block design with three replicates was generated using CycDesigN version 4.0 (VSN International Ltd., Hempstead, UK; blocking efficiency factor = 0.97), with each replicate representing a complete block with 350 treatments (312 families from the eastern gene pool and 38 families from the western gene pool [not included in current study]). Each family was represented once within a replicate and positioned into one of seven incomplete blocks, with each incomplete block consisting of 5 rows x 10 columns. As seedlings from earlier germination batches tended to be taller than those germinated in later batches, families within each incomplete block were randomly ordered with respect to height (i.e. plants within each incomplete block were graded from tall to short then the next incomplete block graded short to tall, etc.) to avoid any confounding issues from shading.

6.2.2.2 Traits measured

To assess the morphological variation among provenances, we measured 20 seedling traits. Many of these traits have been previously used in studies of *E. ovata* (Clucas and Ladiges 1979; Ladiges *et al.* 1981, 1984), with most of these traits believed to have functional significance (Cornelissen *et al.* 2003) and shown in another local system to be associated with provenance differentiation which is believed to reflect home-site climate adaptation (e.g. Gauli *et al*. 2015). Assessment of seedling traits were undertaken at the sixth and tenth node, treating the cotyledon as node zero. Seedling traits were divided into three functional groups: leaf traits, stem traits, and whole seedling development (see Table 6.2 for further details). Briefly, leaf colour, leaf length, leaf broadness, leaf area, and petiole length were measured on fully expanded leaves collected from the sixth node by removing one leaf, which was labelled and then photocopied using a colour flatbed scanner at a dot pixel resolution of 600 dpi. The scanned leaf images were then analysed in the image-processing program ImageJ (Abràmoff *et al.* 2004) using a modified version of the ObjectJ macro (https://sils.fnwi.uva.nl/bcb/objectj/index.html). The red, green and blue colour spectrum of each leaf were assessed using the modal value of five 5 mm diameter random samples of the leaf lamina and the proportion of red, green and blue saturation was calculated following Mizunuma *et al.* (2014). The average thickness of the lamina was measured by taking two thickness measurements 5 mm in from the leaf margin on either side of the midrib at the widest point of the leaf lamina using digital callipers. Specific leaf area (SLA) was also calculated as the area of the fully expanded leaf from sixth node divided by dry weight of that leaf after being dried in a 60 °C oven for 72 hours (Cornelissen *et al.* 2003).

Table 6.2. Leaf, stem, and whole seedling developmental traits measured on *Eucalyptus ovata* seedlings grown in the glasshouse progeny trial. Shown are the grand mean (n = 892) and 95% confidence intervals (CI) for each trait (untransformed), a description of the trait measured, the distribution and unit of the trait, and the transformation (where needed) of the trait to optimise the assumption of normality and homogeneity of the residual variance in the mixed effects models.

Seedling trait	Mean	95% CI	Description	Type, unit	Transformation
Leaf traits					
Proportion alternating leaves	0.41	(0.0, 0.6)	The proportion of a seedling with phased changed leaves (i.e. opposite to alternate leaves up the stem)	Proportion	-
Leaf crenulation	0.48	(0.0, 1.0)	The presence/absence of crenulated (wavy) leaf margins	Binary	-
Leaf thickness	0.14	(0.1, 0.2)	The average thickness of the lamina either side of the midrid measured at the widest point of the leaf	Continuous, mm	-
Leaf length	6.14	(3.7, 8.6)	Length of lamina from tip of leaf to start of petiole	Continuous, cm	-
Petiole length	0.38	(0.0, 0.8)	Length of petiole from start to the point of attachment on the stem	Continuous, cm	-
Leaf red saturation	0.3	(0.3, 0.3)	Saturation of lamina red colour [1]	Proportion	sqrt(x)
Leaf green saturation	0.5	(0.4, 0.5)	Saturation of lamina green colour [1]	Proportion	-
Leaf blue saturation	0.2	(0.2, 0.3)	Saturation of lamina blue colour [1]	Proportion	-
Leaf broadness	0.56	(0.4, 0.8)	Degree of leaf broadness calculated as the ratio between maximum lamina width and lamina length	Ratio	-
Leaf ovateness	0.4	(0.3, 0.5)	Degree of leaf ovateness calculated as the ratio between the distance from the lamina base to the widest point and lamina length	Ratio	-
Specific leaf area	0.16	(0.1, 0.2)	Specific leaf area calculated as the area of the leaf (lamina and petiole) divided by the dry-weight of the leaf	Continuous, $mm^2\ mg^{-1}$	-
Number of expanded nodes	10.16	(7.3, 13.6)	Number of fully expanded nodes, where the first lignotuber node is node 0	Continuous, count	logit(x)
					-
Stem traits					-
Stem angularity	0.47	(0.0, 1.0)	The presence/absence of round stems	Binary	-

Continued from page 117

Seedling trait	Mean	95% CI	Description	Type, unit	Transformation
Stem oil gland development	0.18	(0.0, 1.0)	The presence/absence of oil glands along the stem	Binary	-
Stem redness	0.32	(0.0, 1.0)	The presence/absence of red stem colouration	Binary	-
Stem diameter	5.56	(3.4, 7.9)	Stem diameter measured at node 0 (cotyledons)	Continuous, mm	-
Proportion of internodes	0.19	(0.1, 0.3)	The proportion of the seedling stem with internodes relative to total seedling height	Proportion	-
Relative lignotuber size	0.77	(0.0, 1.9)	The difference between the width of the lignotuber and perpendicular stem width, divided by the perpendicular stem width [2]	Ratio	sqrt(x)
Whole seedling development					- -
Relative lateral length	0.18	(0.0, 0.7)	Length of the longest lateral relative to total height of seedling		-
Relative growth	10.77	(0.5, 31.7)	The difference between total height of seedling at the first and second scoring		sqrt(x)

[1] Leaf colour saturations were calculated following Mizunuma *et al.* (2014) as $S_{red} = N_{red}/(N_{red} + N_{green} + N_{blue})$ $S_{blue} = N_{blue}/(N_{red} + N_{green} + N_{blue})$ $S_{green} = N_{green}/(N_{red} + N_{green} + N_{blue})$, where *S* the saturation of that colour and *N* is the values of the red, green, and blue channels. Colour saturations were calculated using the average of six random 5 mm diameter samples across the leaf lamina. For each of the six samples, the modal colour value was used.

[2] Relative lignotuber size was calculated following Ladiges (1974) as $lignotuber = (DN_{ligno} - DN_{stem})/DN_{stem}$ where *DN* is diameter.

6.2.2.3 Data analysis

To test for variation in morphological traits among provenances (Figure 6.1a), we assessed the evidence for the null hypothesis that provenances do not show differentiation in morphology, tested using mixed effects models fitted with the *lme4* package (Bates *et al.* 2014) in R (R Core Team 2016). The following model was fitted to each response variable (y), treating replicate (rep) as a fixed effect (boldface) and provenance as a random effect (italics):

$$y = \mu + \mathbf{rep} + provenance + family(provenance) + batch + iblk(rep) + \varepsilon \quad (1)$$

where *family(provenance)* is the family effect nested within provenance (hereafter family), *iblk(rep)* is the incomplete block effect nested within replicate, and ε is the residual error. Continuous response traits were fitted assuming a Gaussian distribution with an identity link function. Response traits with a binary outcome were fitted assuming a Bernoulli distribution with a logit link function. Normality and homogeneity of the residual variance were visually assessed for each fitted model, with the response traits transformed (Table 6.2) where necessary to meet the assumptions of the mixed effects models. Pearson residuals were also plotted against each factor in the model to assess for patterns and lack of fit (Zuur and Ieno 2016). The random effect of provenance and family were assessed using a one-tailed likelihood ratio test based on maximum likelihood estimation by comparing twice the log likelihood difference between a model fitted using equation (1) and one with the provenance or family term removed, which follows a Chi-square distribution with 1 degree of freedom.

To test for spatial autocorrelation (i.e. whether neighbouring provenance are more similar than non-neighbouring provenances) among provenances for each response trait, provenance arithmetic means were calculated by pooling across replicates and families. To determine the geographic distance between provenances, the great circle distance among provenance pairs was calculated

using the Delaunay triangulation links between the geographic coordinates of the provenance centroids (Table 6.1), undertaken with the 'tri2nb' and 'nbdist' function of the *spdep* package (Bivand *et al.* 2008) in R. To account for potential gene flow (migration) between neighbouring provenances, a list of general inverse-distance weights was passed to the 'nb2listw' function to calculate the standardised neighbourhood distances. This process allowed the sum of the weights to vary according to the number of neighbouring provenances (Bivand *et al*. 2008). Spatial autocorrelation in provenance trait means was assessed using Moran's *I* as the test statistic and its significance tested using a permutation bootstrap (Monte Carlo) test creating 10,000 simulations of the *I* statistic.

To determine whether a trait that showed significant ($P < 0.05$) provenance variation was under divergent selection (Figure 6.1a), we assessed whether the quantitative trait inbreeding coefficient (Q_{ST}; Whitlock 2008) exceeded neutral expectations (F_{ST}). The Q_{ST} for each trait was estimated using variance components from a model fitted to equation (1) using the average information Residual Maximum Likelihood (REML) algorithm in ASReml-R (Butler *et al.* 2009), following Steane *et al.* (2006):

$$Q_{ST} = \frac{\sigma_p^2}{\sigma_p^2 + 5\sigma_f^2}$$

where σ_p^2 and σ_f^2 are the provenance and family within provenance variance components respectively. $5\sigma_f^2$ is twice the pooled additive variance within provenances assuming a 30% selfing rate (Hodge *et al.* 1996), which is close to the average outcrossing rate reported for eucalypt species (Byrne 2008). Standard errors for estimates of Q_{ST} were calculated using an expanded Taylor series (Gilmour *et al.* 2009). To determine whether seedling traits were under putative divergent selection, Q_{ST} was compared against the maximum putative neutral microsatellite inbreeding coefficient F_{ST}.

As an estimate of F_{ST} for *E. ovata* was not available, we used the maximum value for any microsatellite locus reported for *E. pauciflora* (Gauli *et al.* 2014) and *E. obliqua* (Bloomfield *et al.* 2011) in Tasmania, both of which have similar continuous distribution and provenance structure as the eastern gene pool of *E. ovata*. In this case, we used an F_{ST} of 0.05 found for *E. pauciflora*. Following Dutkowski and Potts (2012), the one-tailed likelihood ratio test of Q_{ST} being significant greater than F_{ST} was tested by comparing an unconstrained model to a model constrained to $Q_{ST} = F_{ST}$ by:

$$\frac{\sigma_a^2}{\sigma_p^2} = \frac{1 - F_{ST}}{5F_{ST}}$$

The ratio was 0.38 for the maximum F_{ST} value of 0.05. Taking a conservative approach, only values of Q_{ST} significantly greater than F_{ST} at $P < 0.001$ were interpreted as signalling putative divergent selection (Whitlock 2008; Edelaar and Björklund 2011).

To determine whether home-site altitude and climate covaried with morphological traits found to be under putative divergent selection (Figure 6.1a), least-square means for seedling traits (calculated by fitting provenance as a fixed effect in equation (1) using the *lme4* package in R) under putative divergent selection were modelled using a Generalised Additive Model (GAM), undertaken with the *mgcv* package (Wood 2006) in R as:

$$y = \alpha + f_1(lat, long) + f_2(predictor) + \varepsilon \qquad (2)$$

where $f_1(lat, long)$ is a bivariate thin-plate smoother function of latitude and longitude to account for spatial structure and $f_2(predictor)$ is a thin-plate smoother function for the altitude/climate predictor variable. The degrees of freedom for the smoother function was estimated using generalised cross validation. In cases where the least-square means were proportional, the estimate of the degrees of freedom was optimised using REML, assuming a beta distribution. Both altitude and

the maximum temperature of the warmest week [TMXWW] have been previously hypothesised as key drivers shaping functional trait variation in the co-occurring *E. pauciflora* (Gauli *et al.* 2015), and indeed were identified in Chapter 2 (Appendix A4) and Chapter 3 (Appendix B3) of this thesis as important predictors of *E. ovata*'s distribution. Thus, altitude and TMXWW were tested as *a priori* predictors of selection in *E. ovata* using equation (2). The relative influence of climate without spatial effects was also fitted by removing the $f_1(lat, long)$ term from equation (2), where the difference between the full model and one fitted using only altitude or TMXWW is the component explained by space. Furthermore, to determine whether any additional climate variables could better predict provenance responses, a second GAM model was fitted using equation (2) by fitting $f_2(predictor)$ as a thin-plate smoother function fitted sequentially for each of the 26 ANUClim derived temperature (not including TMXWW), precipitation, and radiation bioclimatic variables discussed above (Appendix D1). Significance levels were Bonferroni adjusted to control for inflated type-1 error due to multiple testing.

To determine whether the traits that showed signals of divergent selection represented independent responses to the selection agent (Figure 6.1a), we fitted pairwise bivariate models to equation (1) using ASReml-R, which allowed the estimation of both the among-provenance (r_{prov}) and within-provenance genetic (r_{family}) correlations. The covariance structure for each random effect were estimated using the CORGH argument by setting the starting values for parameter estimates using the variance components from the univariate models and fixing the starting values for the incomplete block nested within replicate term ($iblk(rep)$). Following Jordan *et al.* (1999), correlations were estimated as:

$$r_{1,2} = \frac{\sigma_{1,2}}{\sqrt{\sigma_1^2 \sigma_2^2}}$$

where $r_{1,2}$ is the correlation coefficient between trait 1 and trait 2, $\sigma_{1,2}$ is the covariance between trait1 and trait 2, and $\sqrt{\sigma_1^2 \sigma_2^2}$ is the square-root of the variance component for each trait. The significance of the among-provenance (r_{prov}) and within-provenance (r_{family}) bivariate correlations were tested using a two-tailed likelihood ratio test.

6.2.3 Defining the genetic space and aligning with climate

To determine the 'adaptively-enriched genetic space' (Table 6.3 [on pg. 125]; Figure 6.1b) that summarised the maximum variation among provenances of the eastern gene pool of *E. ovata*, we used a linear discriminant analysis (LDA) undertaken with the 'discrimin' function of the *ade4* package (Dray and Dufour 2007) in R. This genetic space was defined using only independent ($P(r_{1,2}) < 0.001$), significant morphological traits that showed evidence of putative divergent selection. The significant ($P < 0.05$) linear discriminant axes (CVs) were identified using the Pillai-Bartlett trace statistic, calculated using the 'MANOVA' function in R. The significant CVs were then used to calculate a pairwise Euclidean distance between provenance centroids, which is analogous to a generalised Mahalanobis distance.

To determine the strength of isolation-by-distance and home-site climate in driving provenance differences in functional traits, the relationship between the Mahalanobis distance matrix of provenance differences (as calculated above) and the Euclidean distance matrix of geographic, altitude, and climate between provenances were assessed using a Mantel test (Mantel 1967), undertaken with the 'mantel' function of the *ecodist* package (Goslee and Urban 2007). The climate distances were calculated based on normalised values of the seven independent bioclimatic variables (see below). The matrix of pairwise geographic distance was transformed using the natural logarithm to account for dispersion in the spatial scale (Rousset 1997). The Mantel test assessed the null hypothesis that the dissimilarities in the Mahalanobis distance matrix are different to the dissimilarities in the Euclidean distance matrices, using a permutation test creating 10,000

simulations of the Pearson *r* statistic. We further used partial Mantel tests to examine the relationship between the Mahalanobis distance matrix and climate once geographic distance and altitude were taken into account. The significance of the partial Mantel test was assessed using a permutation test that randomised the rows and columns of one of the dissimilarity matrix 10,000 times, whilst leaving the other dissimilarity matrices unpermuted (Goslee and Urban 2007). Autocorrelograms of Mahalanobis distance against geographic, altitude and climate distances were also produced using the 'mantel.correlog' function of the *vegan* package (Oksanen *et al.* 2017) to identify the scale over which dissimilarities change, with significance of the Mantel correlation Bonferroni adjusted to account for inflated type-1 error.

To 'climatically align the adaptively-enriched genetic space' (Figure 6.1b; Table 6.3), a canonical correlation analysis of principal coordinates (CAP; Anderson and Willis 2003; Anderson and Robinson 2003) was undertaken using the PERMANOVA sub-module of the PRIMER software (Anderson *et al.* 2008). This analytical procedure was used as it is a widely accepted approach to derive linear assocations between a set of trait variables and a set of environmental variables (e.g. Steane *et al.* 2014). The climatic variables used for the CAP analysis were selected from the 27 bioclimatic variables mentioned above retaining only one of a highly inter-correlated set of variables ($r > |0.7|$; Dormann *et al.* 2013). Correlations were assessed on normalised climate variables using the Pearson correlation test, undertaken with the 'cor.test' function in R on provenance-level means. This process resulted in a subset of seven independent bioclimatic variables that represented provenance home-site temperature (isothermality [TIT], minimum temperature of the coldest week [TMNCW], maximum temperature of the warmest week [TMXWW], mean temperature of the warmest quarter [TWMQ]), precipitation (mean precipitation of the wettest quarter [RWETQ], mean precipitation of the driest quarter [RDRYQ]), and solar radiation (radiation of the wettest quarter [RRWETQ]). The selected climate variables were normalised to a unit variance and a Euclidean

distance matrix was calculated in PRIMER, and then aligned with the trait Mahalanobis distance matrix using CAP.

Table 6.3. Conceptual description of the evolutionary and spatial landscapes derived in the current study, including a definition of each landscape/surface, key reference, and associated figure for each landscape/surface type where applicable.

Name of surface/landscape	Definition	Reference	Associated figures
Evolutionary landscape			
Adaptively-enriched genetic space	The linear combination of morphological traits that maximise the differences among provenances in a multidimensional discriminant space, using only traits showing signals of divergent selection	This study	-
Climate-aligned genetic space	The linear combination of independent axes through the multidimensional point cloud from the 'genetic space' that maximise the correlation with a set of environmental variables, such as climate.	Anderson *et al* 2008; Steane *et al.* 2014; this study	Figure 6.5
Performance landscape	The mean population performance of two or more phenotypes defined using the independent discriminant axes from the 'genetic space'	Arnold 2003	-
(Climate) transfer function	The performance of multiple provenances as a function of the dissimilarity between a population and a site. Here, it is formulated as the difference between home-site climate and trial-site climate.	Matyas 1994; Rehfeldt *et al* 1999	Figure 6.8a
Provenance transfer landscape	The mean provenance performance as a function of the home-site environment as defined by the independent climate indices (eigenvectors) shaping the 'climate-aligned genetic space' *	This study	Figure 6.8b
Spatial landscape			
(Climate) selection surface	The predicted spatial surface of selection that is modelled using the climate indices (eigenvalues) from the 'climate-aligned genetic space'. At equilibrium this surface would represent the predictive spatial distribution of the adaptive component of the phenotype	This study	Figure 6.6a,b

* In the present case these climate indices maximise the correlation between the glasshouse phenotypes and a set of environmental (climate) variables

CAP is a classic approach to finding independent axes of variation through a multidimensional point cloud (in this case the 'adaptively-enriched genetic space') that maximises the correlation with a set of environmental variables (i.e. the normalised bioclimatic variables). The optimal number of axes, *m*, was selected by minimising the leave-one-out residual sum of squares. In the present case, two independent directions of provenance variation were identified with high squared canonical correlations with climate vectors. The weights (eigenvalues) of the seven bioclimatic variables on these vectors were used to calculate 'climate indices', which were then used to predict and map the 'climate selection surface' (Table 6.3) of the eastern *E. ovata* in Tasmania. The climate indices represent independent facets of the climatic variation which is strongly associated with adaptive variation among provenances in seedling traits assessed. These two indices were then used to (i) spatially map the predicted current and future patterns of climate adaptation across the geographic range of the eastern *E. ovata* gene pool, and (ii) relate provenance performance in a common garden field trial (see below) to home-site climate. Spatial raster calculations and mapping were undertaken using the *raster* package (Hijmans 2016) in R.

The spatial and temporal changes in the climate index values were mapped using contemporary and future climate rasters obtained from the Climate Futures for Tasmania project (Corney *et al.* 2010) at a spatial resolution of 30 seconds (*ca.* 0.8 km). The baseline (1976-2005 'contemporary') climate surfaces were developed using ANUClim version 6.1 (Xu and Hutchinson 2012). Future projections of these seven variables were obtained from a dynamically downscaled model using six GCMs (ECHAM5/MPI-OM, CSIRO Mk 3.5, GFDL-CM2.0, UKMO HadCM 3, GFDL-CM2.1 and MIROC3.2 (medres)) for three future time periods that represented the 30-year average of 2010-2039, 2040–2069, and 2070–2099 (hereafter 2020s, 2050s, and 2080s) (see Corney *et al.* 2010 for further details). The six GCMs were selected by Corney *et al.* (2010) as they reasonably replicated current patterns in temperature and precipitation across south-eastern Australia, and also modelled

credible representations of the El Niño Southern Oscillation (Smith and Chandler 2010). The future climate projections were developed assuming a high emission and minimal mitigation scenario (SERS A2, IPCC 2013). Future changes in the climate indices were firstly predicted for each GCM and then averaged to give a mean prediction for each future period studied (i.e. 2020s, 2050s, and 2080s). Predicting the mean climate indices beyond the adaptive range of the eastern gene pool of *E. ovata* was constrained by limiting the mapped surface to the minimum and maximum climate index values calculated for the 2185 occurrence records of *E. ovata* in eastern Tasmania obtained from the Natural Values Atlas (http://www.naturalvaluesatlas.tas.gov.au/; accessed 18 April 2017).

6.2.4 Relating predicted climate adaptation to provenance performance

6.2.4.1 Field trial establishment details

To evaluate whether predicted climate adaptation to home-site of provenances affects field trial performance and transfer distances, we studied early establishment success and growth in a multi-provenance field trial established in the dry, northern Midlands region of Tasmania. Two remnant provenances of *E. ovata* adjacent to the field trial were used as the local seed sources (CON1 and CON2, Table 6.1). The common garden field trial was established in August 2014, 15 km south-east of Cressy (E147.138˚, S41.828˚, hereafter referred to as 'Cressy'; Figure 4.2 in Chapter 4). The trial was planted on a geographically central, low altitude (185 m above sea level) site at the drier limits of the species distribution (Figure 6.2; Figure 3.4 in Chapter 3). The site was previously agricultural pasturelands surrounded by remnant strips of eucalypt woodlands comprising of *E. amygdalina*, *E. viminalis* and *Acacia dealbata*. Since the emergence of pre-industrial warming in the Southern Hemisphere (1959 - Abram *et al.* 2016), mean annual temperatures have significantly increased at this site (0.01 °C per year; $F_{1,104} = 39.2$, $P < 0.001$) but there has been no significant trend in mean annual precipitation (-0.43 mm per year; $F_{1,104} = 1.0$, $P = 0.32$) (Appendix D2; Appendix D3).

The 17 ha trial site was surrounded by a deer proof fence with two hot-wires (electric) to exclude exotic and native browses. The soil was ripped (3 m distance between rip lines) and mounded in early April 2014 using a bulldozer and savannah plough then treated with a knockdown herbicide (Glyphosate plus Simazine™). A month prior to planting, the site was again cultivated and a Glyphosate™ was applied a second time. The trial comprised of 360 open-pollinated families from 51 native provenances (including all families represented in the glasshouse trial described above), of which 317 families represented the 45 eastern provenances of *E. ovata* and 43 families represented the six western provenances of *E. ovata* (not included in current study). Families were germinated as above, and were pricked out into two 40 celled HIKO™ (HV93) trays. Family trays were randomised in an indoor growing area of the commercial nursery, before being transferred outside after 10 weeks. Prior to planting, families were arranged in a resolvable row-column (20 x 18) experimental design created using CycDesigN version 4.0 (VSN International Ltd., Hempstead, UK; row-column efficiency factor = 0.89), with eight complete non-contiguous replicate blocks and families represented once per replicate block. Seedlings were planted with Potipuki No. 55 tree planters with their root ball approximately 2 cm below the soil surface to prevent desiccation (Close and Davidson 2003). Rows (rip lines) were 3 m apart and seedlings were planted 4 m apart along the rows.

6.2.4.2 Field trial performance measures and data analysis

Provenance performance was assessed using measurements of survival, tree height (cm), and reproduction after the second growing season (February, 2017). Reproduction was measured as the presence/absence of buds and/or capsules on surviving individuals. As only a subset of families were studied (the eastern Tasmanian provenances), the trial was analysed as a randomized complete block design. The following model was fitted for each performance measure (y), treating replicate (*rep*), provenance, and family nested within provenance (*family(provenance)*) as a random effect (italics):

$$y = \mu + rep + provenance + family(provenance) + \varepsilon \quad (4)$$

where ε is the residual error. Height was fitted assuming a Gaussian distribution with an identity link function. Response traits with a binary outcome (survival and reproduction) were fitted assuming a Bernoulli distribution with a logit link function. Normality and homogeneity of the Pearson residual variance were visually assessed as detailed above, with no transformations required. The significance of *provenance* and *family(provenance)* variance components was assessed using a one-tailed likelihood ratio test as detailed above.

To determine if provenance establishment success and subsequent performance were related to differences between the provenance home-site and trial climate, dissimilarities in the two dimensional space defined by the two climate index scores (see above) were calculated using the Standardised Euclidean Distances (Williams *et al.* 2007). The relationship, defining the 'climate transfer function' (Table 6.3), was modelled using Generalised Additive Models (GAMs) fitted using the *mgcv* package in R using the following model:

$$y = \alpha + f_1(SED) + \varepsilon$$

where *y* is the provenance least-square mean performance from the field trial (i.e. survival [backtransformed], height, reproduction [backtransformed]) calculated by fitting provenances as a fixed effect in equation (4) and $f_1(SED)$ is a thin-plate smoother function applied to the climate dissimilarity. The response to the two-dimensional surface defined by the two climate indices themselves was modelled by fitting:

$$y = \alpha + f_1(CI_1, CI_2) + \varepsilon$$

where $f_1(CI_1, CI_2)$ is a bivariate thin-plate smoother function applied to both the first and second climate indices. The degrees-of-freedom for the thin-plate spline was estimated using generalised cross-validation. Normality and homogeneity of the Pearson residual variance were visually assessed following Zuur and Ieno (2016).

6.3 Results

6.3.1 Provenance differentiation

Results from the mixed effects models found 15 of the 20 seedlings traits demonstrated significant variation among provenances and family within provenances (Table 6.4), clearly indicating a strong genetic basis to provenance differentiation in the eastern gene pool of *E. ovata*. The variance components accounted for 1.2% [relative growth] to 59.8% [stem oil gland development] of the provenance variation and 4.8% [leaf ovateness] to 25.3% [leaf broadness] of the family within provenance variance (data not shown). The analysis of spatial structure (using Moran's *I*) found significant autocorrelation among provenances for eight of the 20 seedling traits with values for *I* ranging from -0.07 to 0.44 (Table 6.4; Appendix D4), indicating proximal provenances are more similar than expected through chance alone. Most of the spatial structuring in the seedling traits appears to be concentrated in the Tasmanian Midlands, with seedlings from these provenances tending to have broader leaves, larger lignotubers, and greater growth increments between the two scoring periods (Figure 6.3). Nevertheless, following logical progression presented in Figure 6.1a, five of the 20 seedling traits that were assessed were removed from further analysis as they showed no significant provenance variation.

6.3.2 $Q_{ST} - F_{ST}$ comparison

The observed estimates of quantitative differentiation among provenance (Q_{ST}) for the 15 seedling traits ranged from 0.04 (relative growth) to 0.49 (stem oil gland development) (Table 6.4). The Q_{ST} values for eight of the 15 seedling traits were significantly greater than expected based on putatively neutral microsatellite differentiation (F_{ST} = 0.05) (Table 6.4), signalling divergent selection. The mean Q_{ST} for the eight seedling traits under putative divergent selection was 0.19 and the overall mean was 0.14 for the 15 traits showing significant provenance variation.

Table 6.4. Genetic parameters for *Eucalyptus ovata* in Tasmania for (i) the leaf, stem, and whole seedling developmental traits studied in the glasshouse, and (ii) the survival, height, and reproduction traits from the field trial at Cressy. Shown are the random effect of provenance and family using a chi-square one-tailed likelihood ratio test, the quantitative coefficient of differentiation (Q_{ST}) and standard error, the one-tailed likelihood ratio test (LRT) that $Q_{ST} = F_{ST}$, and Moran's *I* testing for spatial structure. Seedling traits are described in Table 6.2. Significance is shown after each test statistic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant ($P > 0.05$). The grey highlighted rows represent the functional traits that have significant provenance variation and a highly significant $Q_{ST} > F_{ST}$ comparison based on the LRT test.

Data set	Trait	Provenance	Family	Q_{ST} (± SE)	LRT	Moran's *I*
Glasshouse trial	**Leaf traits**					
	Proportion alternating leaves	0.7 ns	16.8***	0.02 ± 0.02	6.3 *	0.01 ns
	Leaf crenulation	5.8 **	5.5 **	0.11 ± 0.08	51.5 ***	0.00 ns
	Leaf thickness	25.0 ***	14.1 ***	0.15 ± 0.07	21.0 ***	0.20 *
	Leaf length	34.5 ***	56.1 ***	0.11 ± 0.04	23.2 ***	0.33 **
	Petiole length	20.4 ***	32.1 ***	0.09 ± 0.04	10.6 **	0.36 **
	Leaf red saturation	10.7 ***	4.6 *	0.12 ± 0.08	7.2 **	-0.07 ns
	Leaf green saturation	6.1 **	4.8 *	0.10 ± 0.07	3.4 ns	0.02 ns
	Leaf blue saturation	6.9 **	22.5 ***	0.06 ± 0.03	0.6 ns	-0.04 ns
	Leaf broadness	37.0 ***	59.1 ***	0.11 ± 0.04	27.2 ***	0.41 ***
	Leaf ovateness	2.6 ns	1.8 ns	0.10 ± 0.10	1.7 ns	0.25 **
	Specific leaf area	9.7 ***	15.3 ***	0.08 ± 0.05	2.5 ns	-0.06 ns
	Number of expanded nodes	26.7 ***	26.6 ***	0.11 ± 0.04	15.7 ***	0.14 ns
	Stem traits					
	Stem angularity	34.8 ***	3.7 *	0.30 ± 0.16	182.2 ***	0.00 ns
	Stem oil gland development	62.5 ***	4.6 *	0.49 ± 0.19	406.7 ***	0.22 *
	Stem redness	2.8 *	3.8 *	0.09 ± 0.08	14.4 ***	0.19 *
	Stem diameter	1.4 ns	43.0 ***	0.02 ± 0.02	13.2 ***	0.04 ns
	Proportion of internodes	2.3 ns	35.2 ***	0.02 ± 0.02	8.2 **	0.11 ns
	Relative lignotuber size	20.9 ***	19.4 ***	0.11 ± 0.05	12.9 ***	0.44 ***
	Whole seedling development					
	Relative lateral length	4.9 *	3.9 *	0.11 ± 0.09	3.7 ns	0.01 ns
	Relative growth	1.6 ns	4.3 *	0.04 ± 0.05	0.1 ns	0.25 **
Field trial						
	Survival	0.5 ns	0.7 ns	0.14 ± 0.43	0.0 ns	-0.14 ns
	Height	5.9 **	85.3 ***	0.04 ± 0.02	1.8 ns	0.20 *
	Reproduction	0.58 ns	22.5 ***	0.02 ± 0.03	46.6 ***	0.39 ***

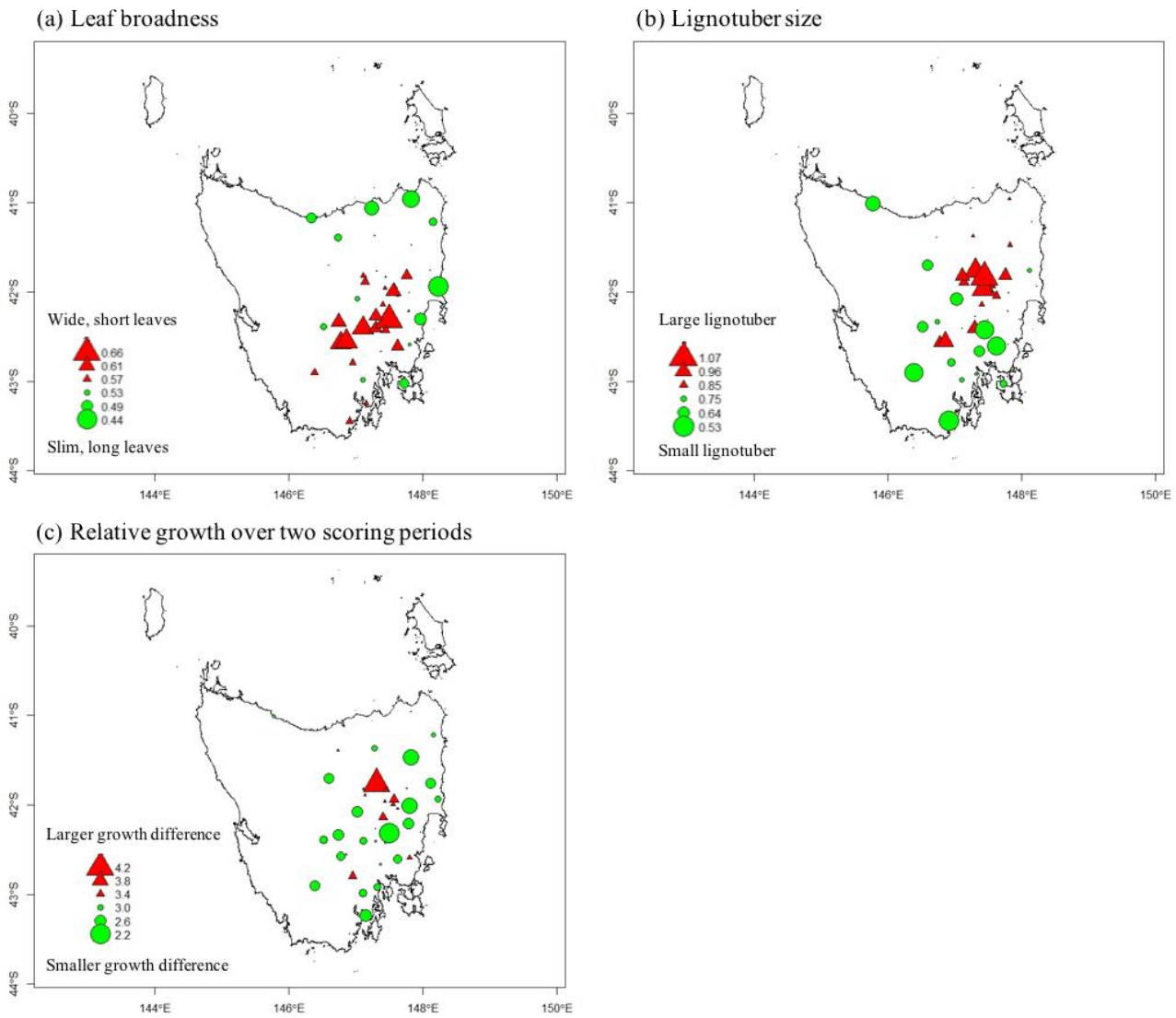


Figure 6.3. Geographic variation in traits showing highly significant spatial variation among the provenance means based on Moran's *I*. Shown are leaf broadness (a), lignotuber size (b), and relative growth during the two scoring periods (c), plotted using the arithmetic mean for the 45 provenance of *Eucalyptus ovata* sampled in Tasmania. The larger the red triangle the greater the mean provenance trail value is above the grand mean and the larger the circle the more the mean provenance trait value is below the grand mean. The provenance mean values show a clear clustering of high values (i.e. larger red triangles) in the Midlands region of Tasmania.

6.3.3 Environmental correlations

The Generalised Additive Models (GAMs) revealed a significant ($P < 0.05$) association between the provenance home-site altitude and variation in five of the eight remaining seedling traits, with altitude accounting for 0% to 28% of the variation in provenance means alone (Table 6.5). For example, leaf thickness, stem angularity and stem oil gland development increased with altitude and the number of expanded nodes and lignotuber development decreased (Table 6.5; Figure 6.4). As the home-site maximum temperature of the warmest week (TMXWW) was weakly correlated with home-site altitude ($r = -0.34$, $P = 0.02$), it was treated as an independent component of the environment. Home-site TMXWW was significantly associated with provenance variation in six of the eight seedling traits, accounting for 7% to 56% of the variation in provenance means alone (Table 6.5). Provenances from warmer (TMXWW) home-sites tended to have seedlings with larger lignotubers and increased number of nodes expanded, but decreased leaf crenulation, leaf thickness, stem angularity and stem oil gland development (Table 6.5; Figure 6.4). Fitting the same GAM as above using all the bioclimatic variables except TMXWW ($n = 26$), showed that after a Bonferroni adjustment of the significance levels to minimise type-1 error, rarely did a single climate variable explain more of the variance in the provenance means than TMXWW alone (Appendix D5). Indeed, the best identified climate variables tended to be temperature variables that were generally strongly correlated with TMXWW (data not shown).

Table 6.5. Association of altitude (m above sea level) and maximum temperature of the warmest week (TMXWW, °C) with the functional trait variation among provenances identified as under putative divergent selection (i.e. $Q_{ST} > F_{ST}$). Shown is the functional trait, the general slope of the curve (when significant), and the estimated degrees-of-freedom (eDF) of the thin-plate spline, the significance of the thin-plate spline for altitude and TMXWW after accounting for spatial effects, the percent (%) of variation explained (R^2_{full}) by the model including space (bivariate thin-plate spline function of latitude and longitude), and the percent (%) of variation explained ($R^2_{variable}$) by the predictor variable (altitude and TMXWW) without space effects. Seedling traits are described in Table 6.2. Significance is shown after each test statistic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant ($P > 0.05$).

Trait code	Relationship	Curve	eDF	Test statistic	R^2_{full} (%)	$R^2_{variable}$ (%)
(a) Altitude (m a.s.l.)						
Leaf crenulation	-	linear	1.00	$\chi^2 = 2.07$ ns	23	na[1]
Leaf thickness	positive	cubic	1.83	$F = 16.13$ ***	46	26
Leaf length	-	linear	1.00	$F = 0.03$ ns	62	12
Leaf broadness	-	quadratic	2.80	$F = 2.18$ ns	79	28
Number of expanded nodes	negative	linear	1.00	$F = 10.79$ **	41	7
Stem angularity	positive	linear	1.00	$\chi^2 = 10.38$ **	45	na[1]
Stem oil gland development	positive	linear	1.00	$\chi^2 = 30.63$ ***	73	14
Relative lignotuber size	negative	linear	1.00	$F = 15.70$ ***	64	21
(b) Maximum temperature of the warmest week (˚C)						
Leaf crenulation	negative	linear	1.00	$\chi^2 = 8.15$ **	22	7
Leaf thickness	negative	linear	1.00	$F = 23.76$ ***	42	27
Leaf length	-	linear	1.00	$F = 0.38$ ns	62	23
Leaf broadness	-	cubic	4.51	$F = 2.18$ ns	68	14
Number of expanded nodes	positive	cubic	2.71	$F = 5.37$ **	47	30
Stem angularity	negative	linear	1.00	$\chi^2 = 14.17$ ***	45	12
Stem oils gland development	negative	linear	1.00	$\chi^2 = 53.34$ ***	53	18
Relative lignotuber size	positive	linear	4.49	$F = 11.69$ ***	65	56

[1] Model failed to converge when fitting only a thin-plate smoother function for altitude

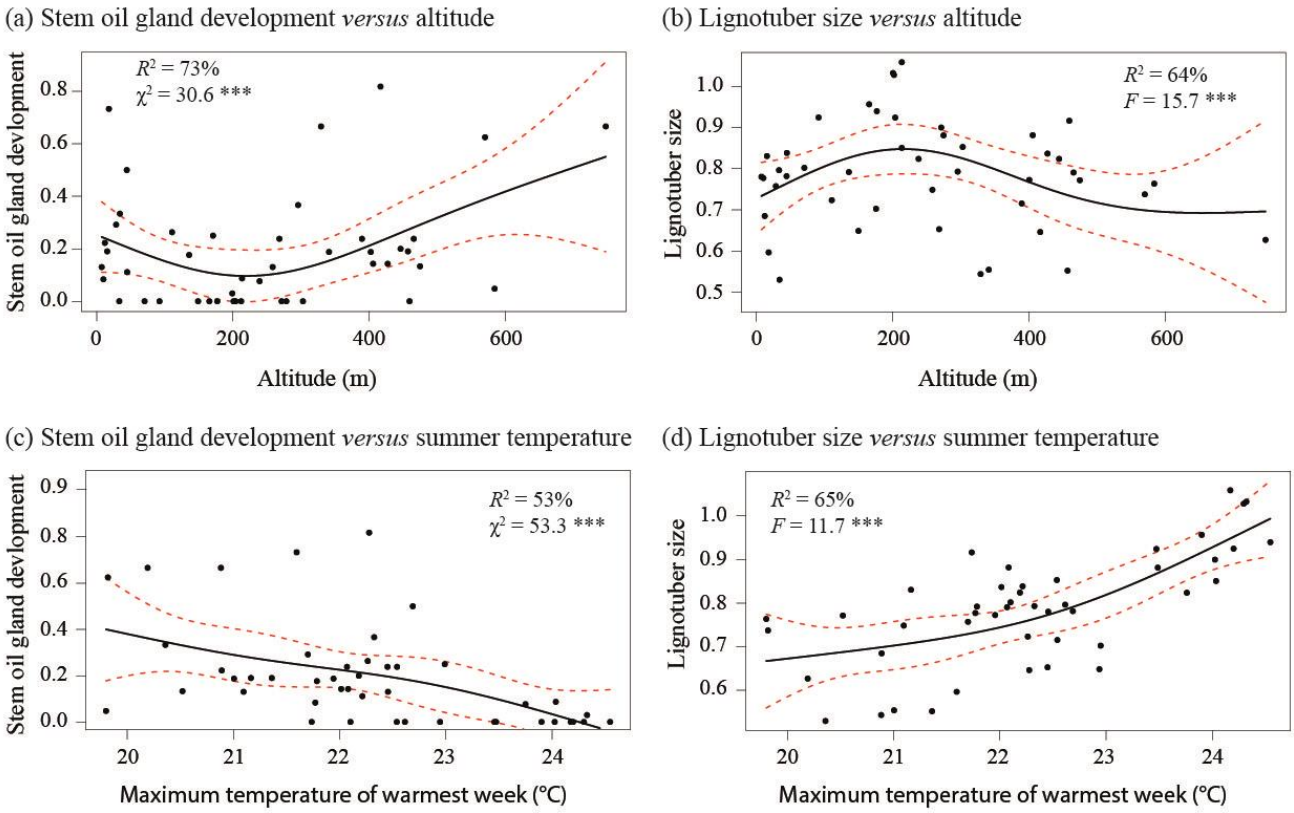


Figure 6.4. Regressions from the generalised additive model of the provenance least-square means against altitude (top row) and maximum temperature of the warmest week (bottom row) for stem oil gland development (left column) and lignotuber size (right column). The solid black line corresponds to the model fit through the provenance means after accounting for the bivariate spatial effects. The red dashed-lines represents the 95% confidence interval for the model fit. The black points are the mean trait values for the 45 provenances of *Eucalyptus ovata* from Tasmania.

6.3.4 Genetic correlations

In many cases the pairwise genetic correlations between the eight seedling traits demonstrated parallel responses to the selection gradients occurring across the eastern gene pool of *E. ovata* in Tasmania (Table 6.6 [on pg. 138]). The absence of significant pooled family within provenance correlations argue these correlated patterns are independent responses to selection (i.e. not due to shared genes or genetic linkage). The only exception was the negative association between leaf length and leaf broadness that were highly significantly ($P < 0.001$) correlated at both levels. These are clearly allometrically related traits, and to reduce the redundancy in the suite of seedling traits studied, leaf length was removed from further analyses. Seedlings from provenances with large relative lignotubers tended to also have less crenulated leaf margins, thinner leaves, increased

number of nodes with expanded leaves, rounder stems, and less stem oil gland development (Table 6.6 [on pg. 138]). While the density of leaf oil glands (count per $1cm^2$) was not included in the present study due only a subset of plants being assessed, it was significantly positively correlated at the provenance-level with the development of stem oil glands ($r = 0.85$, $P < 0.001$; data not shown), suggesting that variation in the development of stem oil glands is indicative of a general increase in seedling defensive chemistry. The negative genetic correlation of the development of stem oil glands with both the number of nodes with expanded leaves and lignotuber size (Table 6.6 [on pg. 138]) suggests a trade-off between defensive and growth/recovery traits.

6.3.5 Adaptively-enriched genetic space

The significant variation among the 45 provenances of *E. ovata* in the seven remaining seedling traits identified above was summarised using a linear discriminant analysis (Pillai trace statistic = 1.1, $F_{44,788} = 3.9$, $P < 0.001$). Ninety-three per cent of the cumulative variance was explained by five significant ($P < 0.001$) discriminant axes (Appendix D6), and was used to define the adaptively-enriched genetic space. The Mahalanobis distances among provenances in this adaptively enriched genetic space were significantly correlated with dissimilarity in (log) geographic distance (Mantel $r = 0.29$, $P < 0.001$), altitude (Mantel $r = 0.15$, $P = 0.02$), and particularly climate (Mantel $r = 0.44$, $P < 0.001$). Autocorrelograms revealed that provenances within (i) 27 km of each other (Mantel $r = 0.12$, $P < 0.001$), (ii) 34 m of altitude (Mantel $r = 0.06$, $P = 0.06$), or (iii) 2.7-units of climate distance (Mantel $r = 0.21$, $P < 0.001$) showed above average similarity in their functional traits than would be expected by chance alone. Similarly, provenances within less than 0.5 ˚C difference in TMXWW (Mantel $r = 0.18$, $P < 0.001$) shared greater than average similarity in seedling functional traits than provenances with greater TMXWW dissimilarities. Importantly, the dissimilarities in the climate distance were still significantly associated with the dissimilarities in the Mahalanobis distance matrix after taking into account the (log) geographic distances between provenances as well

as altitude (partial Mantel $r = 0.35$, $P < 0.001$). This result clearly identifies climatic variables as directly associated with provenance differences in seedling phenotype.

6.3.6 Environmental alignment of the adaptively-enriched genetic space

The Mahalanobis distance matrix among provenances in the adaptively-enriched genetic space was aligned with a set of seven independent climate variables that represented facets of the home-site environment grouped into temperature, precipitation, and radiation variables, undertaken using a Canonical Correlation Analysis of Principal Coordinates (CAP). There was only two orthogonal dimensions of the significant phenotypic variation among provenances which aligned with variation in the climate variables, and population centroids varied continuously (i.e. clinally) along these dimensions (Figure 6.5). The first direction of adaptive provenance variation (CAP1: squared canonical correlation, $\delta^2 = 0.65$, $P < 0.001$) accounted for 35% of the variation in the Mahalanobis distance matrix. Provenances with increasing values along CAP1 (hereafter the arid-adapted phenotype and abbreviated to $CAP1_{ARIDITY}$) tended of occupy home-site environments that received less precipitation during the driest quarter (RDRYQ; $r = -0.88$, $P < 0.001$) and hotter maximum temperatures (TMXWW; $r = 0.79$, $P < 0.001$). The opposing precipitation and temperature vectors were consistent with adaptation to an aridity selection gradient. Provenances from increasingly arid environments tend to have larger lignotubers and an increased number of nodes with expanded leaves. Provenances from more mesic and cooler environments tended to have greater stem oil gland development, increased stem angularity, thicker leaves and increased crenulation along leaf margins.

Table 6.6. Pairwise genetic correlation between provenances and families within provenance for the eight seedling traits of *Eucalyptus ovata* showing signals of putative divergent selection (i.e. $Q_{ST} > F_{ST}$ – see Table 6.4). Seedling traits are described in Table 6.2. Significance is shown after each correlation coefficient. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant ($P > 0.05$).

Morphological trait	Level	Morphological trait						
		Leaf thickness	Leaf length	Leaf broadness	Number of expanded nodes	Stem angularity	Stem oil gland development	Relative lignotuber size
Leaf crenulation	Provenance	0.20 ns	0.33 ns	-0.06 ns	-0.47 ns	0.70 *	0.99 ***	-0.94 **
	Family	0.50 ns	0.33 *	-0.02 ns	-0.02 ns	-0.05 ns	-0.07 ns	0.10 ns
Leaf thickness	Provenance		0.22 ns	0.10 ns	-0.25 ns	0.65 **	0.44 *	-0.82 **
	Family		0.29 ns	-0.01 ns	-0.16 ns	-0.19 ns	0.03 ns	0.46 ns
Leaf length	Provenance			-0.82 ***	-0.06 ns	0.41 ns	0.35 ns	-0.62 *
	Family			-0.42 ***	-0.16 ns	0.08 ns	-0.17 ns	0.13 ns
Leaf broadness	Provenance				0.23 ns	-0.29 ns	-0.29 ns	0.25 ns
	Family				0.12 ns	0.12 ns	-0.18 ns	0.05 ns
Number of expanded nodes	Provenance					-0.59 **	-0.48 **	0.74 **
	Family					-0.22 ns	-0.34 *	0.12 ns
Stem angularity	Provenance						0.69 ***	-0.80 **
	Family						0.35 ns	-0.01 ns
Stem oil gland development	Provenance							-0.94 ***
	Family							-0.02 ns

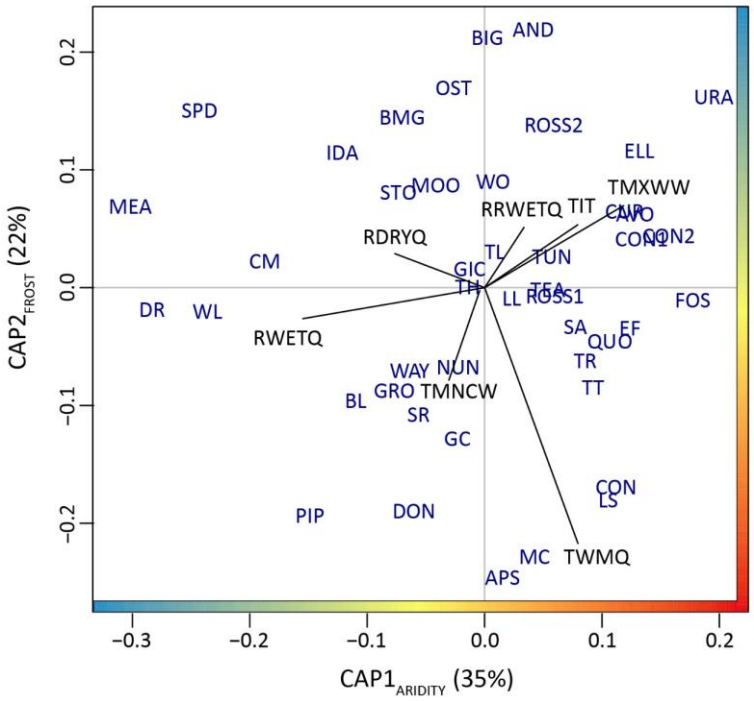


Figure 6.5. Provenance variation among the 45 *Eucalyptus ovata* provenances for seven independent seedling traits under putative divergent selection (i.e. $Q_{ST} > F_{ST}$) within the climate-aligned adaptively-enriched genetic space (Table 6.3). This space was aligned using independent components of the home-site climate undertaken with a canonical correlation analysis (CAP), and accounted for 57 % of the phenotypic variance among provenances. The colour-scale along the x-axis corresponds to the increasing aridity from blue to red along the first canonical axis ($CAP1_{ARIDITY}$) and the colour scale along the y-axis corresponds to increasing frost from read to blue along the second canonical axis ($CAP2_{FROST}$). Provenance codes are given in Table 6.1. Also shown in the two-dimensional CAP space is a biplot of the climate vectors (black lines; maximum temperature of the warmest week, TMXWW; minimum temperature of the coldest week, TMNCW; temperature of the warmest quarter, TWMQ; isothermality, TIT; precipitation of the westest quarter, RWETQ; precipitation of the driest quarter, RDRYQ; radiation of the wettest quarter, RRWETQ)

The second main direction of adaptive provenance variation (CAP2, $\delta^2 = 0.60$) accounted for 22% of the variation in the Mahalanobis distance matrix (Figure 6.5). Provenances with increasing values along CAP2 (hereafter the frost-adapted phenotype and abbreviated to $CAP2_{FROST}$) tended of occupy home-site environments with lower minimum temperature during the coldest week (TMNCW; $r = -0.88$, $P < 0.001$), lower temperature of the warmest quarter (TWMQ; $r = -0.77$, $P < 0.001$) and higher irradiance during the wettest quarter (RRWETQ; $r = 0.44$, $P = 0.003$), indicative of adaptive variation along a frost selection gradient. These provenances tended to have thicker leaves that were much broader than provenance from home-sites that are likely to have a lower prevalence of frost.

6.3.7 Climate selection surface

To visualise the contemporary climate selection surface, the climate indices (vectors, CI) independently associated with the two-dimensional adaptive change among provenances described by $CAP1_{ARIDITY}$ and $CAP2_{FROST}$ (hereafter termed $CI_{ARIDITY}$ to reflect the 'aridity gradient' and CI_{FROST} to reflect the 'frost gradient', respectively) were extrapolated across Tasmania. This was undertaken by normalising the 30sec raster grid cells from the climate layers using the mean and standard deviations from the original climate data used in the CAP, then solving equations (5) and (6) below

$$CI_{ARIDITY} = (TIT_i \times 0.286) + (TMXWW_i \times 0.454) + (TMNCW_i \times -0.131) + (TWMQ_i \times 0.359) + (RWETQ_i \times -0.656) + (RDRYQ_i \times -0.316) + (RRWETQ_i \times 0.150) \quad (5)$$

$$CI_{FROST} = (TIT_i \times 0.234) + (TMXWW_i \times 0.255) + (TMNCW_i \times -0.335) + (TWMQ_i \times -0.839) + (RWETQ_i \times -0.109) + (RDRYQ_i \times 0.095) + (RRWETQ_i \times 0.208) \quad (6)$$

where *i* is the *i*th grid cell in a climate layer and the constants are the canonical eigenvectors from the CAP. The values of the climate selection surface were truncated to the predicted range in the $CI_{ARIDITY}$ (-3.0 to 2.7) and CI_{FROST} (-3.0 to 2.2) gradient scores for all know observations (n = 2185) of *E. ovata* in eastern Tasmania, using the 95% confidence intervals around the mean gradient value. The Midlands and the eastern coast-line of Tasmania were centres of aridity, with the north-west and mountainous regions in eastern Tasmania predicted more mesic and cooler as expected (Figure 6.6a). There was a clear radial trend in CI_{FROST}, from highly negative scores (less frost prone) in coastal regions particularly in the north of the island to positive scores (frost prone) at high elevation and inland regions (Figure 6.6b). The Midlands of Tasmania was the only region where provenances of *E. ovata* were predicted to grow in environment which was both at the extremes of aridity and frost-prone gradients.

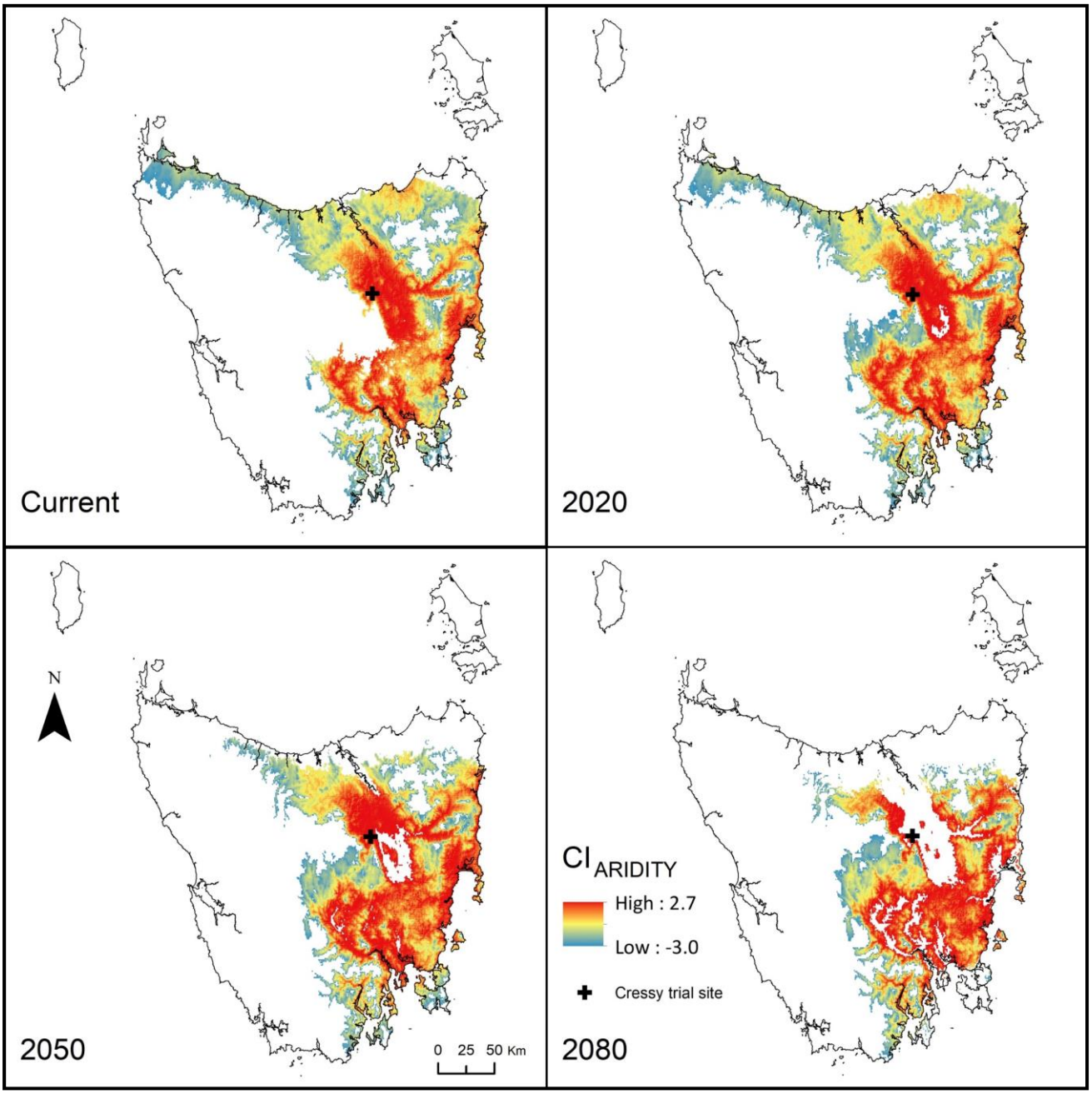
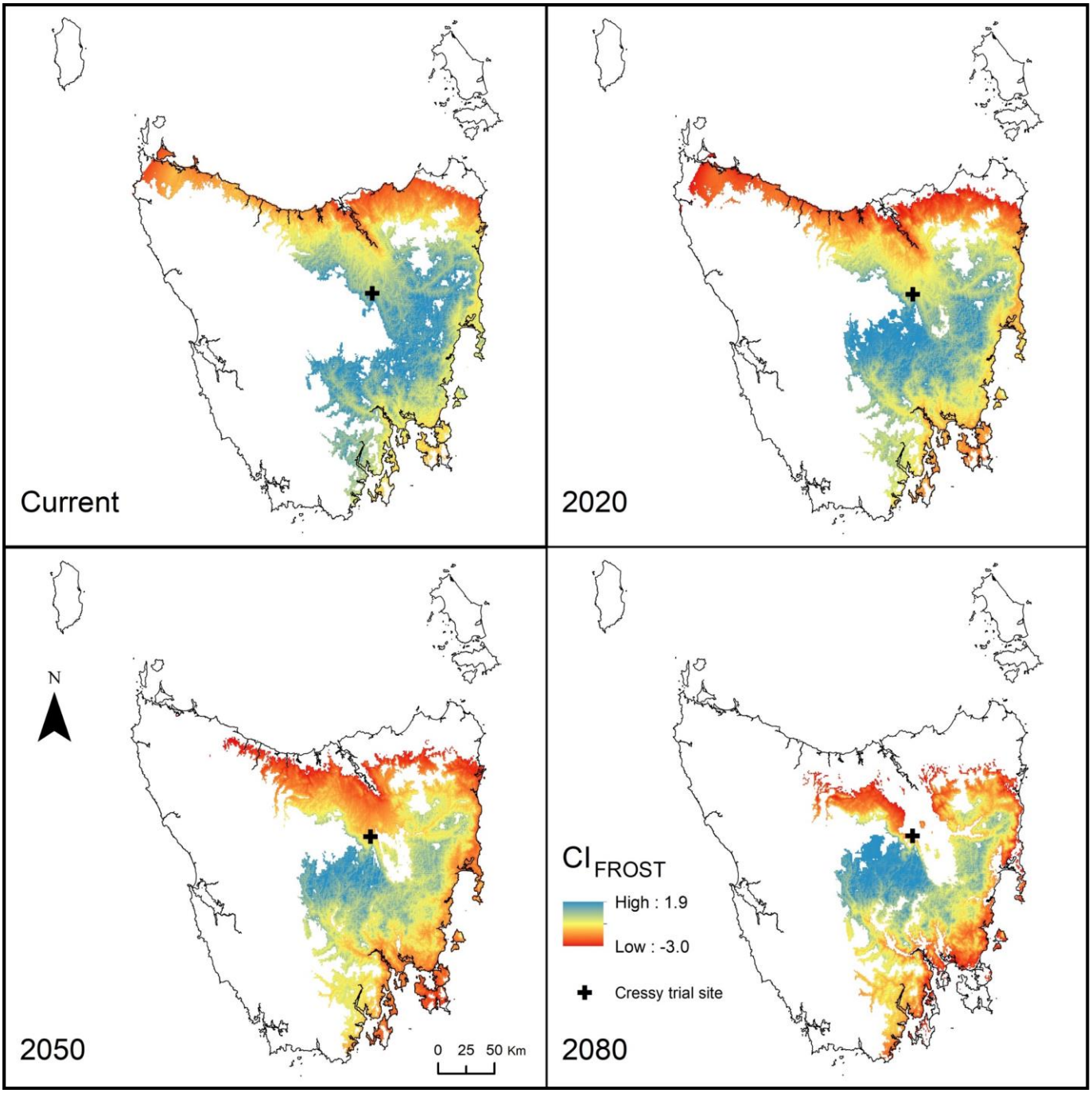


Figure 6.6. Contemporary (1976-2005) and future (2020s, 2050s, and 2080s) predictions of the climate selection surface for the aridity ($CI_{ARIDITY}$) (a) and frost (CI_{FROST}) (b, see over page) adapted phenotypes for *Eucalyptus ovata* in Tasmania. These surface have been clipped using the extent of the frost and aridity surfaces, respectively. The blue surface corresponds to phenotypes adapted to wetter/cooler growing season (a) and increased prevalence of frost occurrences (b). The red surface corresponds to phenotypes adapted to drier/warmer growing season (a) and decreased prevalence of frost (b). The black cross marks the location of the common garden field trail at Cressy.



The two-dimensional climate selection surface for *E. ovata* was then predicted into the future (using the average of values from the GCMs) to visualise the potential re-organisation of the selection surface. Future climate selection surfaces were calculated using equations (5) and (6) above after normalising the future climate projections as previously described. As the climate of Tasmania warms through time, there was a clear intensification and south-eastward expansion of the climate

favouring the arid-adapted phenotype (Figure 6.6a), with an upslope retreat of the climate favouring the frost-adapted phenotype towards the mountains centre of the island (Figure 6.6b). By the 2080s, large component of the *E. ovata*, particularly in the northern Midlands and northern coastal regions is predicted to be beyond the current limits of the environmental gradients becoming too arid or too mild with respect to frosts (Figure 6.6).

6.3.8 Provenance performance in the field trial

Despite covering a diverse range of home-site climates, provenances did not significantly differ in the proportion of plants surviving (χ_1^2 = 0.51, P = 0.48) after two growing seasons at the Cressy field site, with the provenance and family within provenance components accounting for 2.2 and 5.7% of the variance in the model, respectively. The non-local provenances indeed tended to survive on average (mean = 0.87, range = 0.67 [CUR] to 0.96 [TR]) just as well as the local provenances (CON1 = 0.89, CON2 = 0.84) (Figure 6.7). A similar non-significant response was observed for the proportion of surviving individuals that were reproductive (χ_1^2 = 0.58, P = 0.45). However, there was significant variation among families within provenance (χ_1^2 = 22.54, P < 0.001), which accounted for 48.5% of the variance in the model. Variation in growth (height) was marginally significant among provenances (χ_1^2 = 5.88, P = 0.02) and highly significant among families within provenances (χ_1^2 = 58.26, P < 0.001), with the provenance and family within provenance components accounting for 2.7 and 14.4 % of the variance in the model, respectively. However, rather than 'local is best', there was a tendency for the non-local provenances to grow taller on average (mean = 434 cm, range = 344 cm [ROSS2] to 517 cm [GRO]) than the two local provenances (CON1 = 394 cm, CON2 = 392 cm) (Figure 6.7).

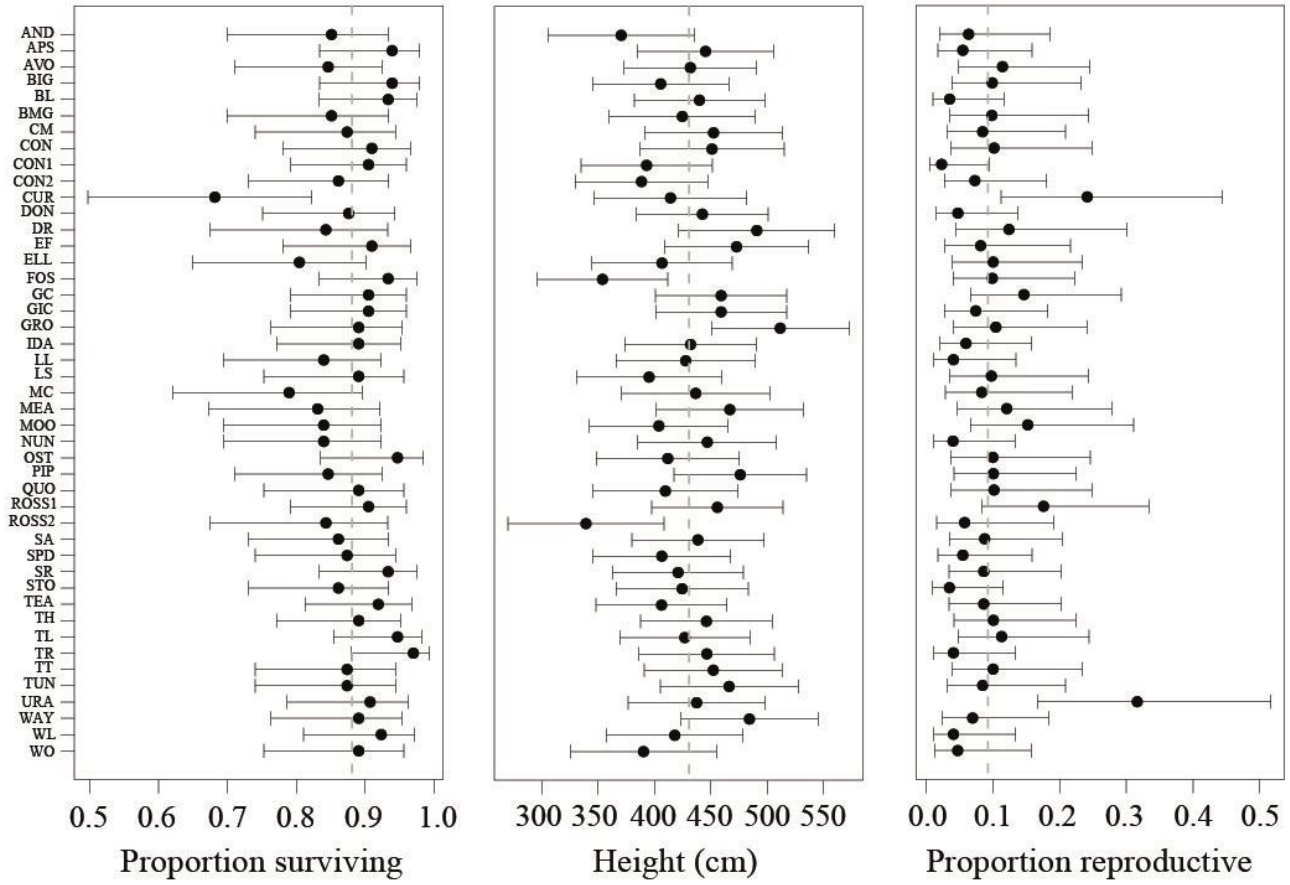


Figure 6.7. Provenance least-square means for survival, height, and reproduction at the Cressy common garden field trial. Black points represent the provenance means and the upper and lower 95% confidence intervals. The local provenances for this trial site were Connorville dam [CON1] and Connorville paddock [CON2] Provenance codes are given in Table 6.1. The grey dashed-line indicates the mean response across all provenances.

6.3.9 Provenance transfer functions

To test whether there was an association of provenance performance (in this case height growth) and phenotypic dissimilarity of the home-site climate to the trial site, we derived a 'climate transfer functions' (Table 6.3) using the Standardised Euclidean Distance. This climate distance was significantly correlated (r = 0.79, P < 0.001) with the climate distance previously used in Chapter 4 (Harrison *et al.* 2017). As expected, we detected little evidence for an association of survival (χ^2 = 0.57, P = 0.45) or reproduction (χ^2 = 1.97, P = 0.42) with the climate distance between the provenance home-site and the trial site. Nevertheless, there was a significant (F = 2.94, P = 0.01)

positive relationship between provenance growth and climate distance from the trial site (Figure 6.8a). However, rather than reflecting a 'local is best' trend, it was the provenances with home-site climates less similar to the trial site which tended to grow taller (Figure 6.8a).

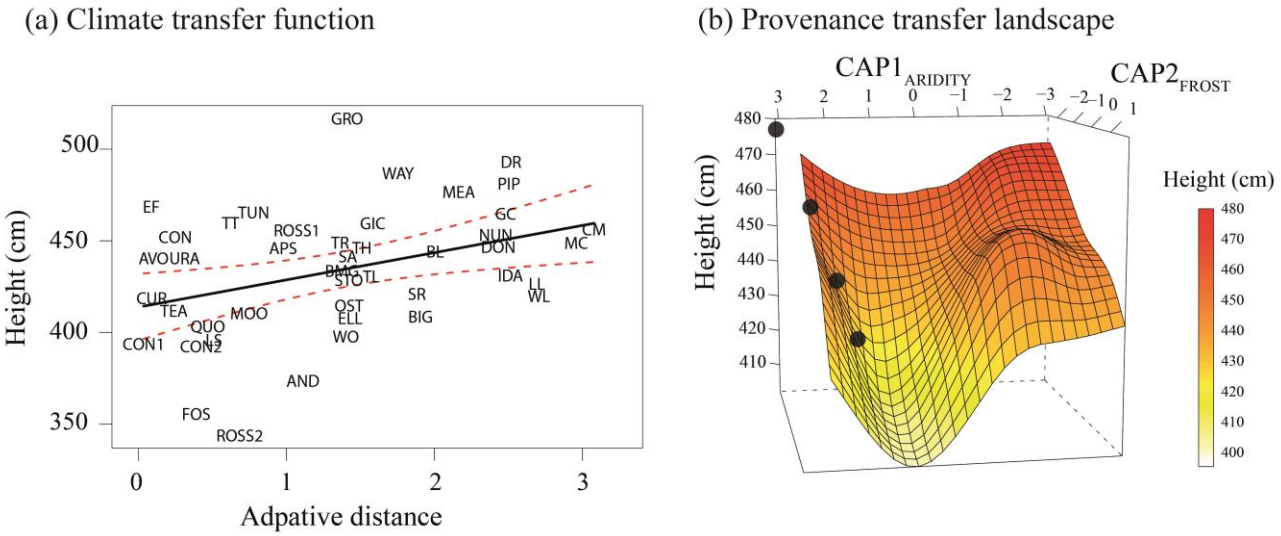


Figure 6.8. Climate transfer function for height growth among the 45 provenance of *Eucalyptus ovata* in Tasmania, using the distance of a provenances mean phenotype ($CAP1_{ARIDITY}$ and $CAP2_{FROST}$) from the optimal predicted for the trial site at Cressy (a) under contemporary conditions. Increasing values along the x-axis in (a) correspond with increasing dissimilarity between a provenance and trial site. Also shown is the provenance transfer landscape for height growth (b). Increasing values along $CAP1_{ARIDITY}$ correspond with home-site climates becoming more hot and dry, whereas increasing values along $CAP2_{FROST}$ correspond with home-site climates becoming more frost-prone. The black points show the predicted optimal phenotype for the trial site at the Cressy for contemporary (1976-2005) and future (2020s, 2050s, 2080s) climates (height only). Provenance codes are given in Table 6.1.

6.3.10 Provenance transfer landscape

The unexpected trend in the provenance transfer function for height growth can be mainly attributed to the response of provenances from less frost-prone environments to have better early growth despite the fact that the test site was more frost prone (i.e. higher values on the frost gradient [$CAP2_{FROST}$]) (Figure 6.8b). Modelling the variation in height growth as a bivariate function of the frost and aridity gradients (defining the 'provenance transfer landscape' – see Table 6.3) showed a marginally significant fit of height growth ($F = 2.09$, $P = 0.05$). Predictions from this model found that 30 of the 45 *E. ovata* provenances had a mean height greater than the current predicted site mean

(Cressy trial site height = 426 cm; Figure 6.8b), a trend also evident in the observed differences in height growth of the provenances relative to the local provenances (Figure 6.7). Eighteen of these predictions were generally from warmer less frost-prone home-sites, while the remaining 12 predictions were from provenances with home-site climates that were frost-prone but cooler-wetter (Figure 6.8b). While the number of frost days averaged over the two growing seasons did not differ markedly from the 1976-2005 contemporary baseline (49 versus 50, respectively), this trend in provenance performance could be at least partly be explained by an increase in the minimum temperature of the coldest week by 0.6 ˚C (Appendix D3). Provenances from home-sites climates most analogous to the projected 2020 and 2050 climates for trial site, were predicted to grow better than the local provenance (Figure 6.8) and were predicted to generally originate from provenances that experienced fewer frosts (i.e. negative values along the frost gradient). No home-sites were analogous to the predicted 2080 climate of the trial site.

The absence of significant differences among the provenances for survival and reproduction, coupled with the better predicted early height growth of provenances occurring in analogous future climates projected for the trial site (black circles in Figure 6.8b), indicates that, under current climate conditions, it is clearly possible to establish (at least up to two years of age) provenances originating from homes-site climates analogous to the future climate of the planting site.

6.4 Discussion

The present study defines and implements a pathway for developing an adaptively relevant provenance transfer landscape that can be empirically validated (through field trials) and used to define (climate) selection surfaces that can be modelled through space and time. Climate change impacts are conceptually standardised by their historical effect on the differences that have evolved among provenances of species under divergent selection. The development of this framework to

guide the climate-adjusted provenancing strategy depends on the demonstration of significant adaptive variation in key functional traits that are associated with the macroclimate of the provenance home-site. The present study reveals two independent facets of the climate that are likely to have shaped selection in seedling functional traits in our study species *E. ovata* in Tasmania. It also predicts major changes in this selection surface under a warming future, with a large component of the species distribution likely to experience novel conditions in terms of more extreme 'aridity' and but less 'frost' severity. While the outlined approach provides a means of weighting and standardising the effects of climate variables, applying this selection surface to provenance transfer guidelines for restoration and reforestation assumes that these differences will eventually translate to equivalent fitness differences among provenances in contemporary and future climates. At this early stage of seedling establishment in the current environment we have yet to see evidence of maladaptation associated with transfers across the provenance transfer landscape.

6.4.1 Climate shapes functional trait variation among provenances

The present study argues that the genetic variation in seedling functional traits has been shaped by variation in climate across the distribution of *E. ovata* on the island of Tasmania. Two lines of evidence support the role of divergent selection in shaping the provenance differences in the studied functional traits. Firstly, several of the traits that showed significant provenance differentiation also showed significant Q_{ST} values exceeding neutral expectations (i.e. $Q_{ST} > F_{ST}$; Whitlock 2008), indicating that different phenotypes are favoured in different environments (Merilä and Crnokrak 2001). While our observed estimates of Q_{ST} trait values are well below those observed in some Northern Hemisphere species (Savolainen *et al.* 2007; Alberto *et al.* 2013), such as Sitka spruce (*Picea sitchensis*, timing of bud set Q_{ST} = 0.89; Mimura and Aitken 2007), our values are within the ranges reported for sessile oak (*Quercus petraea*; Kremer *et al.* 2014) and other eucalypts (Steane *et al.* 2006; Dutkowski and Potts 2012). Our average Q_{ST} of 0.19 for eight seedling traits with

significant $Q_{ST} - F_{ST}$ comparisons was similar to that reported in seedling traits of *E. pauciflora* (0.18, Gauli *et al.* 2015) but slightly than the mean Q_{ST} reported in *E. globulus* (0.13, Steane *et al.* 2006) and in 59 Northern Hemisphere species (0.12; Leinonen *et al.* 2008), and indicates there is considerable divergent selection among provenances (Merilä and Crnokrak 2001). Indeed, the high Q_{ST} observed for the development of stem oil glands (Q_{ST} = 0.49) is indicative of high provenance differentiation in this trait (Alberto *et al.* 2013). Secondly, provenance divergence in functional traits was more associated with climate dissimilarities than with the geographic distances or altitude dissimilarities among provenances. While we cannot dismiss a component of isolation-by-distance driving provenance differences in the functional traits (Lande 1991; Sexton *et al.* 2014), partialling out the effects of geographic distance and altitude still resulted in a highly significant climate correlation, indicating that differences in the home-site climate is likely the driving selective agent. Indeed, univariate analyses showed traits with high Q_{ST} also had strong correlations with the home-site climate and altitude, further supporting the likelihood of climate as a driver of trait evolution (Hansen *et al.* 2012).

6.4.2 Evolutionary response to the climate selection surface

The functional trait variation between provenances of *E. ovata* in Tasmania has likely been shaped by a two-dimension climate selection surface defined by two orthogonal climate gradients – an aridity gradient and a frost gradient – with the provenances means varying clinally along these two gradients. Morphological clines along environmental gradients are well-known in both plants (Reich *et al.* 2003; Etterson 2004; Vitasse *et al.* 2009) and animals (Mullen and Hoekstra 2008), and have been reported for eucalypts (Potts 1985; Gibson *et al.* 1995; McLean *et al.* 2014). In the present case, the lack of evidence for pleiotropy among the functional traits (i.e. significant genetic correlation at both the provenance and family within provenance level) (Anderson *et al.* 2011) suggests that the between-provenance genetic correlations likely reflect independent, parallel

evolutionary responses to increasing home-site aridity and frost (i.e. selective covariance, Armbruster and Schwaegerle 1996; Reich *et al.* 2003). Indeed, our results suggest that provenance variation within *E. ovata* is at least partly explained by the imposition of the two independent phenotypic clines that have evolved in response to the climate selection surface.

ARID-ADAPTED PHENOTYPE The first phenotypic cline was correlated with variation in home-site aridity associated with variation in maximum temperatures and summer rainfall. The adaptive response to this gradient appears to indicate a genetic trade-off between growth (increased lignotuber development and leaf expansion) and defensive traits (decreased development of stem oil glands and increased leaf thickness). The clinal trade-off between growth and defensive traits is difficult to explain with our current data, however, may partly reflect the growth-differentiation balance hypothesis (Loomis 1932, 1953). This hypothesis provides a framework to predict how plants may balance the allocation of resources (i.e. carbohydrates) between growth-related traits (e.g. roots and leaves) and differentiation-related traits (e.g. increased thickness of leaf cuticle and increased secondary metabolites) over a heterogeneous environment (Herms and Mattson 1992; Ayres 1993; Stamp 2003). It also predicts that any environmental factor that slows growth more than photosynthesis will result in the increased allocation of resources to differentiation-related traits (Herms and Mattson 1992; Ayres 1993; Stamp 2003). Indeed, the increased development of defensive traits (stem oil glands and fewer, thicker leaves) is associated with provenances from cooler and presumably slower growing seasons, and such defence of the limited expanded leaves may be an adaptive response to herbivory pressure (Ladiges *et al.* 1984; Potts 1985; Lerdau *et al.* 1994; Moreira *et al.* 2016). Nevertheless, increased lignotuber development is an evolutionary significant adaptation to aridity (Stebbins 1952), and can result in the vegetative recovery of aerial parts of the plant after biotic and abiotic damage (Mullette 1978), such as herbivory, drought, or fire (Lacey 1983; Nicolle 2006b; Clarke *et al.* 2013). Many plant groups show lignotuber development (Clarke *et*

al. 2013), and it is a common feature of most eucalypts (Nicolle 2006b). The adaptive significance of these genetic trade-offs between growth and defensive functional traits to increasing aridity is further supported by the parallel responses observed in the co-occurring species *E. pauciflora* along the same climate gradient (Gauli *et al.* 2015). The likelihood of observing a similar genetic trade-off between growth and defensive traits in two species from different subgenera (Brooker 2000) along the same selection gradients by chance alone is extreme low, and suggests the trade-off between recovery/growth and defence may be an adaptive syndrome (Reich *et al.* 2003) to increasing home-site aridity.

FROST-ADAPTED PHENOTYPE The second phenotypic cline was related to variation in the prevalence of frost at the home-site associated with variation in minimum temperature extremes, growing season temperature and winter radiation. The combination of low temperature and high radiation is a well-known stressor which can lead to photoinhibition in eucalypts (Ball *et al.* 1991; Close *et al.* 2000; Teulieres *et al.* 2007). Increasing home-site frost risk was associated with provenances having thicker and broader leaves. Below-freezing temperatures (i.e. frost) can occur anytime of the year in Tasmania (Jackson 2005), and frosts are well known to cause extensive damage to exposed parts of the plant (i.e. leaves) (Inouye 2000; Teulieres *et al.* 2007), shape eucalypt species distribution boundaries (Davidson and Reid 1985), and provenance differentiation (Barber and Jackson 1957; Ashton 1958; Tibbits *et al.* 1991). The observed clinal variation in these traits likely reflects an eco-physiological response to such extreme temperatures (Jordan and Smith 1995). Indeed, it has been shown that thicker and smaller leaves is a whole-plant strategy to reduce damage to internal components of the leaf in frost-prone sites (Stefanowska *et al.* 1999; Reich *et al.* 2003; Mediavilla *et al.* 2012; Pérez-Harguindeguy *et al.* 2013).

6.4.3 Differential climate adaptation did not adversely impact early establishment

Despite clear evidence for differential adaptations in seedling functional traits, we were unable to detect any evidence of performance maladaptation in early establishment of *E. ovata* after translocating provenance along a gradient of increasing phenotypic dissimilarity from the optimal phenotype predicted for the trial site. This is a promising result for assisted gene flow strategies, such as the climate-adjusted provenancing strategy (Prober *et al.* 2015), as it indicates the potential to establish provenances from future analogous climates in current climatic conditions. However, this result is to some extent unexpected given that the observed adaptive variation in the early life stage traits would suggest differential establishment successes of provenances, one-way-or-another. Several factors may have contributed to this result:

1. *There has been no selection event at the trial site*. Over the studied growth period (2-years) the trial site never experienced a strong selection event, such as extreme temperature (frost or heat stress) or drought stress, with generally favourable growing conditions. Such extreme events have previously revealed significant provenance differences in susceptibility to damage in eucalypts and other forest tree species (Teulieres *et al.* 2007; Dutkowski and Potts 2012; Kreyling *et al.* 2014). Indeed, such events may impact the establishment of provenances that show antagonistic trade-offs (i.e. negative genetic covariance between traits) to the direction of selection (Etterson and Shaw 2001).
2. *The trial site climate has changed*. The observed climate over the two growing seasons at the trial site were on average generally warmer than the baseline contemporary climate (1976-2005). It is possible that the observed climate during the two growing seasons at the trial site has shifted to favour the non-local phenotype. Insights into this hypothesis could be gained by modelling the climate anomaly between the growth period at the trial site and the contemporary climate at each sampled provenance against the performance measures.

3. *Missed critical selection stage in the regeneration niche*. The artificial nature of our experiment (i.e. germination and establishment under ideal and controlled conditions) may have missed critical selective events that may segregate the phenotypic differences among provenances during early establishment. Indeed, in wild population, selection and competition within microsites is often intense during germination events post-disturbances, such as fire (Davis 1991; Purdy *et al.* 2002; Bailey *et al.* 2012).
4. *Lack of competition*. Canopy closure at the trial site has not yet occurred, suggesting a lack of inter- and intra-provenance competition. Indeed, competition through indirect genetic effects on the growth of neighbouring families have been previously shown for *Eucalyptus globulus* after canopy closure (i.e. 4-years; Costa e Silva *et al.* 2013), which highlights the need to consider the dynamics of stand development through time when determining success of translocation plantings.
5. *Fitness consequences of seedling traits not realised until later life stages*. It is possible that the adaptive advantages of the seedling functional traits studied here will not be realised until the adult life stage. For example, Poorter (2007) showed that in light-limited environments the early-age functional leaf traits of 58 forest tree species had long-lasting consequences on the form and shape of the tree, which translated into later-age fitness differences. Nevertheless, the height growth differences observed in the field trial may represent alternative growth strategies to temperature (Way and Oren 2010), with provenances from frost-prone home-sites investing greater resources into below-ground biomass (i.e. roots) than above-ground biomass (Reich *et al.* 2014). Such differences in early-growth strategies of eucalypts (i.e. growing faster) have been shown to be genetically correlated with later-age survival in competitive environments (Chambers *et al.* 1996; Stackpole *et al.* 2010).

6.4.4 Conclusion

This study has demonstrated how a two-dimensional climate selection surface has shaped the clinal variation in seedling functional traits across the eastern gene pool of *E. ovata* in Tasmania. The approach we have undertaken is conceptually similar to the genome-wide scan and outlier detection analysis of Steane *et al.* (2014). While there are advantages in using genome-wide scans to detect signals of environmental adaptation for conservation strategies (Neale and Kremer 2011; Williams *et al.* 2014), both our approach and the approach of Steane *et al.* (2014) still require further validation using field trials. Nevertheless, studying seedling functional trait variation and the associations with home-site environment potentially provides a 'fast track' to bypass the time required to establish and monitor provenance differences in common garden field trials. Indeed, for long-lived organisms, such as forest trees, it can take decades to detect local superiority or maladaptation (Neale and Kremer 2011; Prober *et al*. 2016), which may no longer be an option given the current velocity of climate change (Loarie *et al.* 2009). Our approach has provided a way to identify and weight the importance of macroclimate variables shaping functional trait evolution for predictive tools such as PUCA (Chapter 4; Harrison *et al.* 2017), and provides a way in which to visually represent the historic climate selection surface and model this for current and future climates. Climate selection surfaces will be useful for identifying and matching provenances to sites for adaptive conservation strategies, such as assisted gene flow and climate-adjusted provenancing.

Acknowledgements

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the modified version of the ObjectJ macro for ImageJ that was used to calculate the leaf morphological traits scored in the current study (available at https://sils.fnwi.uva.nl/bcb/objectj/index.html). This study was supported by an Australian Research Council Linkage Grant (LP120200380) in partnership with Greening Australia, and was part of a PhD undertaken by PAH, which was supported through an Australian Government Research Training Program Scholarship (CHESSN: 3404427365).

Chapter 7: General discussion and conclusions

This thesis has advanced knowledge on the conservation and management of the Tasmanian eucalypt flora under future climate change and has provided a framework to guide the establishment of climate-resilient ecological restoration and reforestation plantings. It has used correlative models to provide insights into the predictability of future climate-induced habitat loss and has shown that the current reserve systems in Tasmania provide multiple climate 'safe havens' for eucalypt diversity (Chapter 2). The thesis has identified multiple local and non-local candidate species for regional ecological restoration in Tasmania (Chapter 3) and has provided a tool (Provenancing Using Climate Analogues - PUCA) to identify the most appropriate seed sources along a gradient of environmental (climate) change, whilst considering the potential inbreeding effects occurring in fragmented forests (Chapter 4). During this thesis, short- and long-term experimental trials were established to test the assumptions of the PUCA model and identify the climate components which have shaped adaptive variation among the provenances of the key woodland restoration species *Eucalyptus ovata*. A germination trial showed that provenance home-site climate did not affect seed germination characteristics (Chapter 5). A glasshouse trial was used to develop a novel quantitative genetic modelling approach to identify and weight key climate variables that impact adaptive variation within *E. ovata,* and a common-garden field trial was used to demonstrate that 'climate-ready' provenance can establish under current climate regimes (Chapter 6). The key findings and conclusions from this thesis are presented in the following major points.

7.1 Climate as a major driver of adaptive variation

7.1.1 Proportion of phenotypic variation accounted for by climate

The macroclimate appears to be a major drive of adaptive variation among provenances of *E. ovata,* and indeed accounted for 57 % of the phenotypic variation in seedling traits (Chapter 6 –

variance explained by both $CAP1_{ARIDITY}$ and $CAP2_{FROST}$). The magnitude of this relationship appears to be close to the average of the range reported for forest tree species (*Eucalyptus pauciflora*, $r^2 = 0.22$, Gauli *et al.* 2015; *Eucalyptus tricarpa*, $r^2 = 0.50$, Steane *et al.* 2014; *Quercus berberudufolia*, $r^2 = 0.46$, Riordan *et al.* 2016; *Quercus petraea*, $r^2 = 0.58$, Bruschi *et al.* 2003; *Populus nigra*, $r^2 = 0.16$, Dewoody *et al.* 2015; *Pseudotsuga menziesii*, $r^2 = 0.68$, St Clair *et al.* 2005). However, the proportion of variation accounted by the macroclimate appears to be greater than the range reported for non-tree species (*Arabidopsis thaliana*, $r^2 = 0.09$, Stearns and Fenster 2013; *Echinacea angustifolia*, $r^2 = 0.12$, Still *et al.* 2005; *Pseudoroegneria spicata*, $r^2 = 0.41$, St Clair *et al.* 2013), presumably due to the more direct exposure of forest trees to the macroclimate. Nevertheless, the relationship found for *E. ovata* supports the influential role of the macroclimate in shaping the genetic architecture of phenotypic variation within forest tree species (Linhart and Grant 1996).

The proportion of the phenotypic variation not explained (i.e. the residual variance) by climate is unlikely to be associated with isolation-by-distance effects (Lande 1991; Sexton *et al.* 2014), as the matrix relationship between phenotypic difference and geographic distance among provenances (after factoring out the effect of climate and altitude dissimilarities) was non-significant (Chapter 6). This result could simply reflect the maintenance of large populations whereby random genetic drift has yet to act even in the absence of contemporary gene flow, or alternatively it may reflect the persistence of gene flow between proximal provenances that are within 27 km of one-another (Chapter 6). Nevertheless, the role of neutral processes (such as genetic drift) cannot be dismissed completely as an additional source of variation driving phenotypic differences among provenances (Lande 1976; Willi *et al.* 2007).

There were two key sources of variation that were not accounted for in this thesis that may further improve the association between trait variation in *E. ovata* and the environment. The first is microclimate differences that are often associated with steep environmental gradients occurring across heterogeneous landscapes, such as Tasmania. Microclimate differences have been shown to significantly shape adaptive variation in physiological and quantitative traits (McKay *et al.* 2001; Opedal *et al.* 2015; Stark *et al.* 2017), with, for example, significant trait differentiation occurring over just a few hundred meters within Tasmanian provenances of *E. obliqua* (Wilkinson 2008). The second is edaphic factors, which are well-known selective agents shaping ecotypic variation within plant species (Sambatti and Rice 2006; Wright 2007). Nevertheless, the general lack of fine-scale environmental data (i.e. spatial layers) highlights a key gap in our understanding of how micro-environmental variation shapes *E. ovata* and indeed other forest species, which is integral to understanding the potential positive/negative feedbacks between the macro- and micro-environment on species as climates change (De Frenne *et al.* 2013).

7.1.2 Key climate variables shaping adaptive variation

This thesis provides evidence that the Tasmanian eucalypts may be sensitive to the temperature component of their macroclimate. In particular, the maximum temperature of the warmest week (TMXWW) was identified as an important climate variable throughout this thesis. Not only was TMXWW an important predictor in modelling the distribution of suitable habitat for most of the Tasmanian eucalypts (Chapter 2), and identifying candidate species (Chapter 3) and provenances (Chapter 4) for ecological restoration in the Tasmanian Midlands, it was also found to be significantly associated with adaptive variation among the provenances of *E. ovata* in Tasmania (mean R^2 = 23%, range R^2 = 7% to 56%; Chapter 6). Temperature appears to be a ubiquitous driver of adaptive variation in many forest tree species (Carnicer *et al.* 2013; Moles *et al.* 2014). For example, home-site mean annual temperature, growing degree days, and mean warmest month

temperature are strongly associated with provenance growth differences in species of *Pinus* (Rehfeldt *et al.* 1999; Rehfeldt *et al.* 2002; Wang *et al.* 2006; Mimura and Aitken 2007). Functional traits have also been demonstrated to significantly vary with home-site maximum temperature, including morphological variation in leaf traits of *Quercus berberidifolia* (Riordan *et al.* 2016) and lignotuber development in *E. ovata* (Chapter 6) and the co-occurring species *E. pauciflora* (Gauli *et al*. 2015).

7.2 An adaptive syndrome to home-site aridity

This thesis has revealed a genetic-based 'trade-off' between functional traits measured on seedlings of *E. ovata* (Chapter 6). Here, a 'trade-off' is defined as a negative genetic covariance between two (or more) traits (Roff and Fairbairn 2007). For example, there was a negative genetic relationship between lignotuber development and stem oil gland development, as well as a negative relationship between the number of leaves expanded and stem oil gland development (Chapter 6). The negative genetic covariance's were associated with a provenances home-site aridity, and similar genetic-based trade-offs have been reported for the co-occurring species *E. pauciflora* (e.g. lignotuber development *versus* stem oil gland development - Gauli *et al.* 2015), as well as in the genus *Pinus*. In the latter case, Moreira *et al.* (2016) found *Pinus* species growing in harsh environments tended to grow slower and produce the 'costly' constitutive defensive traits, as opposed to the fast-growth species from resource-rich environments that produced the 'low-cost' induced defensive traits. While the significance of oil gland development on the stem as a defensive trait against natural enemies is not well understood in *E. ovata*, the positive genetic correlation between stem oil glands and density of oil glands in leaves (Chapter 6) suggests it may be indicative of a general increase in defensive chemicals that may infer a defensive advantage in environments that limit growth.

In the present case, the parallel genetic trade-offs observed in two separate lineages of *Eucalyptus* (i.e. subgenus *Eucalyptus* [*E. pauciflora*] and *Symphyomyrtus* [*E. ovata*]; Brooker 2000)

may reflect an adaptive syndrome to increasing home-site aridity (i.e. decreasing summer precipitation and increasing maximum summer temperatures – Chapter 6). This hypothesis is based on three lines of evidence. First, the bivariate correlations between trait pairs (growth/regenerative *versus* defence) observed for *E. ovata* (Chapter 6) and *E. pauciflora* (Gauli *et al.* 2015) show the same antagonistic relationships suggesting a common genetic trade-off to a selection pressure. Second, these antagonistic relationships were strongly associated with the same climate (TMXWW) gradient. Third, there is a mechanistic understanding to these traits whereby increased lignotuber development is an evolutionary significant adaptation to aridity (Stebbins 1952), and increased development of constitutive defensive traits (i.e. stem oil gland development) may be an adaptive response to protect long-lived leaves in resource-limited habitats (Coley 1988; Stamp 2003). It is possible that this 'adaptive syndrome' may reflect the growth-differentiation balance hypothesis (Loomis 1932, 1953), where the pool of resources are allocated to one trait at the expense of another trait (see section 6.4.2 of Chapter 6 for further discussion). While this response has only been demonstrated in two eucalypt species, it is hypothesised that this 'adaptive syndrome' could have evolved as a result of convergent evolution, whereby species from different lineages evolve a similar trait or set of traits in response to the same environmental selection gradient. Nevertheless, in the present case, the possibility of the trade-off between growth/regeneration and defensive traits being conserved since splitting from a common ancestor cannot be dismissed. Further research of this hypothesised adaptive syndrome to aridity is required, as well as further studies to explore its generalities in eucalypts and other plant taxa.

7.3 Different perspectives on the niche space

This thesis has applied two independent approaches to model the distribution of suitable habitat of *E. ovata* to determine the maladaptation risk faced under current and future climate change. The first approach used correlative models, such as habitat suitability models (Chapter 2), which relied on the assumption of Hutchinson's fundamental niche (Hutchinson 1957; Elith and Leathwick 2009).

The second approach used a novel 'quantitative genetic model' that spatially predicted phenotypic trait means arising from relationships between home-site climate and functional traits showing signals of divergent selection (Chapter 6). This approach is conceptually similar to mechanistic modelling (Schoener 1986; Kearney *et al.* 2010) and relied on the assumption that adaptive variation in functional traits has evolved through time in response to environmental selection pressures, resulting in a phenotype that permits a species to survive and reproduce indefinitely (Rosenzweig 1987).

The two modelling approaches showed strong convergence under contemporary (i.e. 1976-2005) climate conditions, with minor discrepancies at the peripheral margins of the predicted suitable habitat range (Figure 7.1a). However, the two approaches diverged in their predictions of suitable habitat by the end of this century (2080s), with the quantitative genetic model predicting a larger component of *E. ovata*'s current distribution in the north and central Tasmania to be outside the 2080s predicted adaptive range of the species, compared to the habitat suitability model predicting a relatively unchanged model from the contemporary (Figure 7.1b). While the large reduction in suitable habitat is consistent with global predictions (Thuiller *et al.* 2011; Lenoir and Svenning 2015) and for eucalypts in general (Butt *et al.* 2013; Gonzalez-Orozco *et al*. 2016), the reason for the contrasting patterns between these modelling approaches under future climate change is difficult to disentangle. Nevertheless, the most likely cause for the observed difference in the future predictions is due to the differential weighting of the climate variables associated with adaptive variation in the quantitative genetic model. Indeed, the quantitative genetic model is more aligned to the adaptive variation along the climate selection gradients than the traditional correlative modelling approach, and it has been shown that incorporating genetic (quantitative and molecular) information into models of suitable habitat can often lead to more realistic climate change predictions (Bush *et al.* 2016; Ikeda *et al.* 2016).

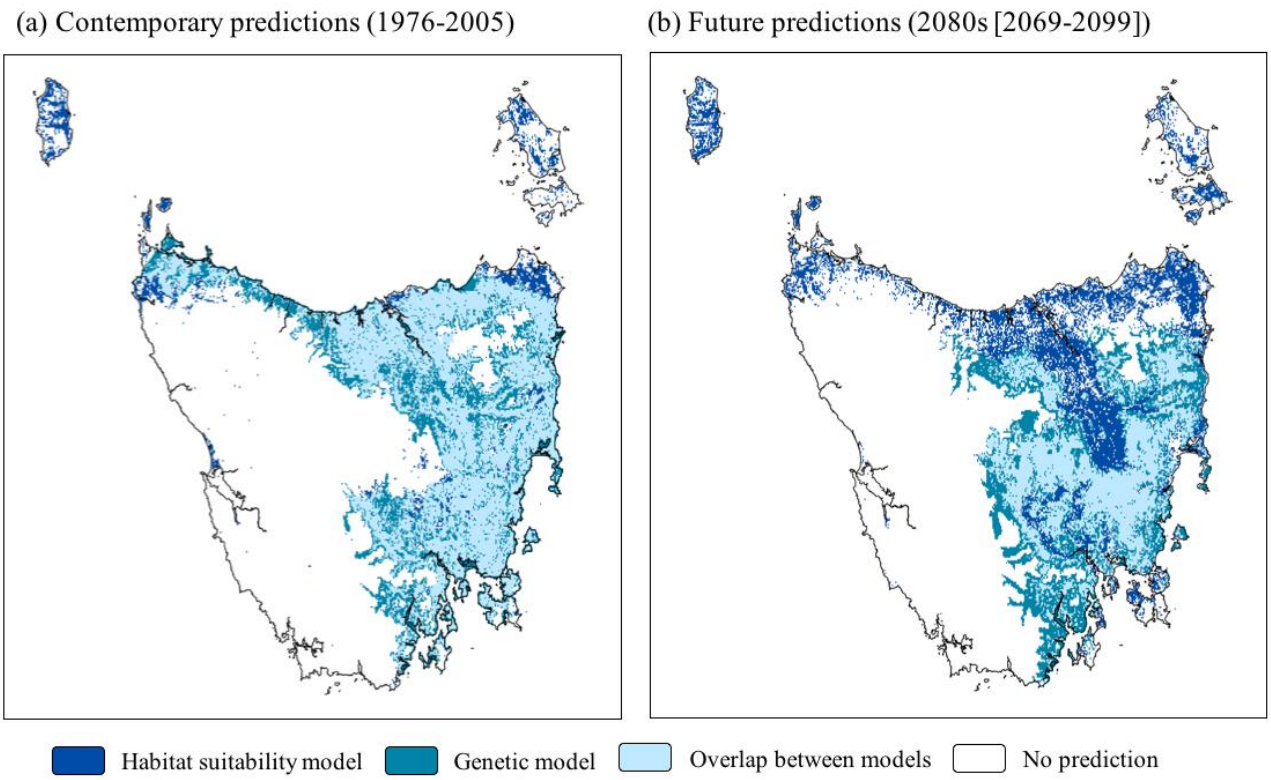

Figure 7.1. Convergence between the two approaches to model the distribution of suitable climate-habitat for *Eucalyptus ovata* in Tasmania under contemporary (1976-2005; a) and future (2080s; b) climate change. The light blue surface shows areas of convergence between the habitat suitability model (Chapter 2) and the quantitative genetic model (Chapter 6), pale blue shows areas only predicted by the quantitative genetic model, and the dark blue shows areas only predicted by the habitat suitability model.

7.3.1 Differences in niche space

A species niche can be conceptually divided into two components, the 'survival niche', and the 'regeneration niche' (Grubb 1977; Bykova *et al.* 2012). The overlap of the survival niche and the regeneration niche (in the presence of competition) can be interpreted as the 'realised niche', which is a discrete hyper-volume within the fundamental niche (Hutchinson 1957). Here, the survival niche includes the 'tolerance niche' (Sax *et al.* 2013) and the regeneration niche includes the 'reproduction niche' and the 'establishment niche' (as conceptualised in Chapter 2). While eucalypts have numerous strategies to persist in unfavourable environments (Pryor 1976), such as the ability to change habit (Hopkins and Robinson 1981) and revert to a juvenile form (Wiltshire *et al.* 1991), the impact of environmental change is likely to be more noticeable in the regeneration niche (Bell 1999; Mok *et al.* 2012).

It is likely that changes in the climate cues for different components of the regeneration niche, such as the timing of flowering (Keatley *et al.* 2002) and the breaking of primary seed dormancy (Nitschke and Innes 2008; Mok *et al.* 2012), may narrow the hyper-volume of the regeneration niche (Erickson *et al.* 2015). Indeed, this is likely to be most noticeable for species that require a cold stratification to break seed dormancy. Mok *et al*. (2012) showed that under future climate change, the modelled regeneration potential of *E. pauciflora* may shift to higher elevations as cold stratification requirements will unlikely be met at lower altitudes. The modelled upslope contraction through time of the 'climate-sensitive' (*sensu* Mok *et al*. 2012) regeneration niche for *E. pauciflora* was consistent with the upslope contraction predicted by the future habitat suitability models for this species in Tasmania (Chapter 2), and provides an independent line of evidence further demonstrating the potential susceptibility of *E. pauciflora* to future climate change. While this thesis hypothesised that *E. ovata* would require a wet-cold stratification to break seed dormancy in high-altitude provenances, Chapter 5 clearly showed that provenance home-site climate did not affect the seed germination characteristics of this species. Furthermore, early results from the field trial found there was significant additive genetic variation in reproductive performance (i.e. presence of buds and capsules) within *E. ovata* provenances (Chapter 6), suggesting there may be genetic variation in the timing of the switch between vegetative and reproductive phases. Depending on the strength of selection (Savolainen *et al.* 2004), reaching reproductive-maturity at an earlier age may increase the number of generations that can establish and thus increase the potential for the provenance to adapt to changes in the climate (Jump and Peñuelas 2005). Nonetheless, these results indicate that the regeneration niche of *E. ovata* is not as climate-sensitive as other species, such as the co-occurring *E. pauciflora* (Mok *et al*. 2012).

7.4 Consequences of being outside of the niche space

It has been widely predicted that many species will be outside their suitable climate-habitat as global climates change. Indeed, large components of the distribution range for most of the eucalypts

in Tasmania were predicted to be outside their modelled suitable climate-habitat by the end of this century (Chapter 2). Aitken *et al.* (2008) described five potential responses a species may exhibit if/when they are outside their suitable climate-habitat:

1. *A 'nothing' response*. A species may be insensitive to the changes in its suitable climate-habitat through time resulting in a neutral impact on fitness. While this is an unlikely response given the global shifts in species range boundaries (Thomas 2010; Chen *et al.* 2011; Feeley *et al.* 2013) and widespread dieback of forests (Allen *et al.* 2010) associated with current climate change, species may have a much wider 'tolerance niche' than expected (Sax *et al*. 2013).
2. *A plastic response*. A species may adjust to the novel environment by changing its phenotypic mean through plasticity. Indeed, phenotypic plasticity in wild populations may aid the evolution of adaptive phenotypes in novel environments through 'de-canalisation' processes (Chevin *et al.* 2010, 2013; Franks *et al.* 2014). However, there will be ecological limitations to phenotypic plasticity, especially for long-lived forest species (Parmesan 2006; Valladares *et al.* 2007) such as eucalypts.
3. *An adaptive response*. A new phenotypic optimum may evolve in response to a selection pressures if there is sufficient standing genetic diversity maintained within provenances. However, local adaptation is a multi-trait function (Aitken *et al.* 2008) and the rate of evolution may be constrained if traits are genetically correlated (Arnold 1992; Etterson and Shaw 2001). Furthermore, the velocity of climate change may be too rapid for evolutionary processes to keep pace (Loarie *et al.* 2009; Gonzalez *et al.* 2012) and result in an adaptation lag (Matyas 1996; Wilczek *et al.* 2014). Nevertheless, the considerable standing genetic variation within provenances of *E. ovata* (Chapter 6) and *E. pauciflora* (Gauli *et al*. 2015) suggests there is evolutionary potential within provenances of these species.

4. *A migration response*. A species may track its suitable climate-habitat by dispersing propagules (i.e. seed and pollen). For sedentary species, such as forest trees, the velocity of climate change may be too quick for migration to keep pace (Burrows *et al.* 2014). Nevertheless, long-distance pollen-mediated dispersal may provide sufficient dispersal of genes across the landscape to keep pace with predicted climate-habitat shifts (Kremer *et al.* 2012).
5. *A local extinction (extirpation) response*. If a species is unable to adapt or adjust its phenotype or migrate, there is likely to be an increased chance of provenance extirpation (Aitken *et al.* 2008; Anderson 2016).

The above five responses are not mutually exclusive, and it is likely that the response of a species will be spatially heterogeneous. For example, the leading or trailing edge may disperse or retreat to favourable climate-habitat whereas other parts of the distribution may show plastic or adaptive responses to the environmental change. Nonetheless, it is likely that as climates warm through time, populations will go through a stage of tolerance up until a maladaptation 'tipping point' is crossed, where a population is unlikely to recover.

7.5 Implications for natural resource management and ecological restoration

Climate change will likely have a profound impact on global ecosystems, and the long-term management of natural resources will require an understanding of the potential impacts faced by species as climates warm (Guisan *et al.* 2013). This thesis has provided a broad insight into the predicted effect climate change will have on the distribution of suitable climate-habitat for the eucalypts of Tasmania (Chapter 2, 6). These climate-niche models provide some of the first broad-scale maps on the spatial redistribution of climate-habitat for the Tasmanian eucalypts, and provides the pathway to target components of the gene pool that are important for the conservation of the species (i.e. predicted to be maladapted under future climates), as well as genetic resources key for the long-term survival of the species (i.e. currently occupying future analogous environments). This

latter point was an additional motivation for developing the Provenancing Using Climate Analogues (PUCA; Chapter 4), as it provides invaluable insights into key regions/provenances for targeted seed collections for *ex situ* conservation strategies such as seed banks (Schoen and Brown 2001). As we approach the first time period of these modelled simulations (i.e. the 2020s), there is an increasing need to establish long-term monitoring plots (e.g. Wood *et al.* 2015 and Caddy-Retalic *et al.* 2017) to monitor potential shift in species boundaries that will provide feedback for adaptive conservation strategies. Indeed, the predictions for the 2020s may already be occurring, with anecdotal evidence suggesting that the recent dieback of *E. viminalis* and *E. globulus* along their northern boundaries in Tasmania was a result of a period of extreme heat stress (Department of Primary Industries Parks Water and Environment 2015), consistent with the predictions from Chapter 2.

Globally, large investments into the ecological restoration of degraded ecosystem are being made in an attempt to restore biodiversity and ecosystem functioning in the face of climate change (i.e. the Bonn Challenge – Verdone and Seidl 2017). However, with the large dependency on local seed and the potential decoupling of local adaptations with selective regimes under current and future climate change, there was a need to devise methods to help the implementation of the various proposed provenancing strategies. This thesis has provided a testable framework to identify 'climate-ready' species and provenances for climate-resilient restoration plantings (Chapter 3, 4). Chapter 3 identified both local and non-local candidate species for restoring the Midlands of Tasmania, several species of which are not currently utilised as restoration species (Table 7.1). Furthermore, Chapter 4 provided the operational-ready program – Provenancing Using Climate Analogues (PUCA) – to test and implement the climate-adjusted provenancing strategy of Prober *et al.* (2015), whilst considering the potential inbreeding within fragmented provenances. It identified several key collection areas that currently maintain provenances of a species within current and future analogous climates predicted for the two northern Midlands restoration sites (Cressy and Ross) (Table 7.1).

Table 7.1. Candidate species of *Eucalyptus* identified in Chapter 3 for ecological restoration in the Tasmanian Midlands and whether that species current distribution is within this region. Also shown is the location of key seed provenances for two restoration sites (Cressy and Ross) predicted across three time periods (Contemporary [1976-2005], 2020s [2010-2039], and 2050s [2040-2069] climate), undertaken using the Provenancing Using Climate Analogues program (PUCA; Chapter 4). The missing data in the 'Key collection areas' represented by a dash denotes species that are not currently deployed as restoration species and were not assessed using PUCA. Collection sites are predicted to be where species are currently occupying analogous climates predicted for the restoration site across three time periods.

Subgenera/Species	Local species to Midland region	Key collection areas		
		Contemporary	2020s	2050s
Subgenus *Eucalyptus*				
E. amygdalina	Yes, whole region	Epping Forest to Oatlands; Hamilton	Epping Forest to Ross; Avoca; Hamilton	Longford; Epping Forest; Avoca
E. pauciflora	Yes, whole region	Longford to Epping Forest to Oatlands; Avoca; Hamilton; Ouse	Longford to Epping Forest to Oatlands; Avoca; Hamilton; Ouse	Longford; Epping Forest to Avoca; Royal George
E. pulchella	Yes, southern region	-	-	-
E. risdonii	No	-	-	-
E. tenuiramis	Yes, southern region	Ellendale; Osterley	Ellendale; Hamilton	Ellendale
Subgenus *Symphyomyrtus*				
E. barberi	Yes, north-eastern region	-	-	-
E. globulus	Yes, southern region	-	-	-
E. ovata	Yes, whole region	Cressy to Epping Forest to Oatlands to Avoca and Royal George; Hamilton; Ouse; Wayatinah; Ellendale	Cressy to Epping Forest to Oatlands to Avoca and Royal George; Hamilton; Ouse; Wayatinah; Ellendale	Longford; Avoca; Royal George
E. rodwayi	Yes, southern region	Arthurs Lake; Cressy; Royal George; Tunbridge; Victoria Valley	Arthurs Lake; Cressy; Royal George; Tunbridge to Tooms Lake	Royal George
E. rubida	Yes, southern region	-	-	-
E. viminalis	Yes, whole region	Cressy to Epping Forest to Oatlands to Avoca and Royal George; Hamilton; Ouse	Cressy to Epping Forest to Oatlands to Avoca and Royal George; Hamilton; Ouse	Launceston; Longford; Epping Forest to Avoca and Royal George

This thesis has also defined a spatial and environmental scale for an operational 'local' provenance of *E. ovata* (Chapter 6). The spatial structuring of adaptive variation among provenance of *E. ovata* showed that provenances within 27 km of another tended to share more similar adaptive traits than expected by chance alone. This spatial operational scale is consistent with the molecular defined operational distance for *E. pauciflora* (27 km, Gauli *et al.* 2014), *Banksia menziesii* (30 km, Krauss *et al.* 2013), and *Dryandra lindleyana* (20 km, Krauss and Koch 2004). An alternative definition for a local provenance was also defined using a measure of climate dissimilarity among provenances using seven climate variables (see section 6.2.3 of Chapter 6), which found provenances that were within 2.7-units of climate distance also tend to share more similar adaptive traits than expected by chance alone. To my knowledge, this is the first operational definition of a local provenance using climate dissimilarities for use in ecological restoration, and provides a critical parameter for PUCA which defines the 'cut-off' transfer distance of a provenance. Indeed, the operational distances of a local provenance for *E. ovata* are less-conservative than the 10 km and 2-units of climate distance used to parameterise the PUCA model in Chapter 4 (Harrison *et al.* 2017), which suggests there may be additional seed sources not identified in Chapter 4.

This thesis has also established multi-provenance trials embedded within the broader restoration plantings across the northern Midlands of Tasmania. These trials are key research facilities that are allowing the experimental testing of the various provenancing strategies to evaluate how they rank relative to the traditional 'local-is-best' provenancing strategy. The early results from these trials are providing evidence that demonstrates it is possible to successfully establish non-local provenances under current climate conditions at the restoration site (Chapter 6). While this is only early establishment data and the general growing conditions since planting were favourable (Chapter 6), it nonetheless signals early empirical support for assisted migration strategies, such as climate-adjusted provenancing (Prober *et al.* 2015). Nevertheless, the extended impacts of such translocations on

remnant vegetation (e.g. outbreeding depression; Costa e Silva *et al*. 2012) and on dependent communities (Sinclair *et al.* 2015) needs further investigation (Bucharova 2016).

7.6 Concluding remarks and future directions

In conclusion, this thesis has provided methodological approaches and the tools required to assist in the identification of the best climate-matched species and provenances for climate-resilient ecological restoration. Further, it has provided additional evidence that supports the role of climate as a putative selective agent shaping adaptive variation in *E. ovata*. While we found little evidence of adaptive differences in performance traits between local and non-local provenance (Chapter 6), this was not a surprising result. Like most forest species, *E. ovata* has a long-generational time, and to detect adaptive differences in the field requires more time and/or extreme selective events such as drought or heat/frost stress. The lack of catastrophic events during the early establishment phase likely resulted in this lack of differences in provenance performance. Therefore, it is too early to tease apart the superiority of local and non-local provenances. The future monitoring of these trials as selective regimes shift with climate change will no doubt provide continued refinement of provenancing strategies for ecological restoration, including transfer distances. Several areas of future research that will further inform the ecological restoration and conservation of the Tasmanian eucalypt flora include:

1. Gaining an understanding of how historical evolutionary processes (such as genetic drift) have shaped neutral molecular variation. This will not only provide further insight into the role of neutral processes in shaping adaptive genetic variation, but will also provide an estimate of genetic diversity and patterns of gene flow within a species. These results together with the habitat suitability models would help to better inform the conservation of a species gene pool, as well as provide an analogous molecular-based operation definition of a local provenance;

2. Detecting genome-wide markers associated with climate adaptation and understanding the relationship of these markers with performance traits from the field trials. This may provide an additional method to 'fast-track' the identification of local adaptation to home-site environments (e.g. Steane et al 2014) which could be used to guide assisted migration strategies, such as climate-adjusted provenancing;
3. Gaining an understanding of how and whether a species interacts with the micro-environment (edaphic factors and microclimate), including gaining insights into how species interact with the the soil microbial communities, how forest species buffer the microclimate from macroclimate warming (De Frenne *et al*. 2013), and how local adaptations are shaped by fine-scale changes across heterogeneous environments;
4. Gaining a better understanding of the combined influences of land-use change (i.e. fragmentation) and climate change on the reproductive biology of the Tasmanian eucalypts (including the spatial structure of reproductive events) to produce models of future reproduction for *ex situ* conservation strategies, such as collect seed for long-term storage (Schoen and Brown 2001). Lastly, determining how various levels of habitat fragmentation impact on outcrossing within and between provenances will assist the decision process for selecting seed sources for ecological restoration.

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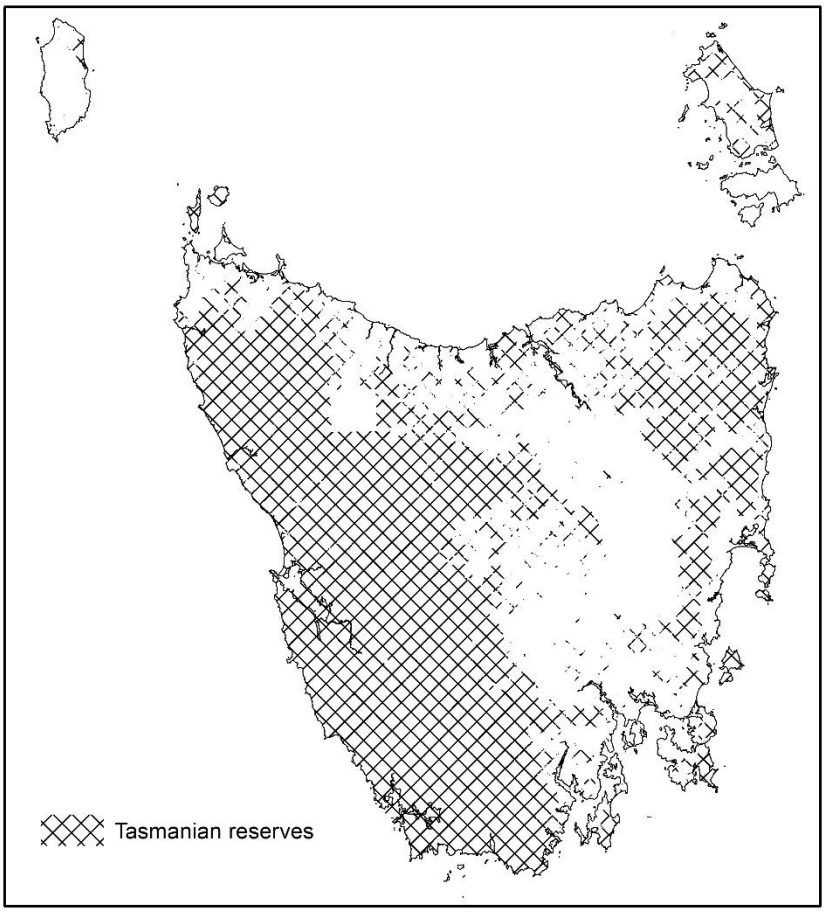
Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution* **7**, 636–645. doi:10.1111/2041-210X.12577.

Appendix A - Supplementary material for Chapter 2

Supplementary material A1

Spatial representation of the 5981 reserves (hatched polygon) used in the current study that resents forest reserves with greater than or equal to 10 ha. Reserves were identified using the Tasmanian LISTmap (http://maps.thelist.tas.gov.au/listmap/app/list/map; accessed 5th Jan 2017).



Supplementary material A2

Model evaluation metrics for the optimised Random Forest model. Models were optimised using the best number of candidate variables (*m*) to use at each node split. The optimised model was selected by minimising the out-of-bag (OBB) error and maximising the discrimination power (Gini index) of the model. Each model was also evaluated based on its ability to correctly classify occurrences (Specificity, type 1 error) and pseudo-absences (Sensitivity, type 2 error). Evaluation statistics for each species were estimated from the confusion matrix that was derived from the 30% of the test data that did not contribute to the training of the Random Forest model. Species have been ordered by their informal classification (Potts and Williams 1996) and their subgenera classification (*Eucalyptus*: 'Ashes' and 'Peppermints'; *Symphyomyrtus*: 'Black gums', 'Blue gums', 'White gums', 'Yellow gums', 'Alpine white gums').

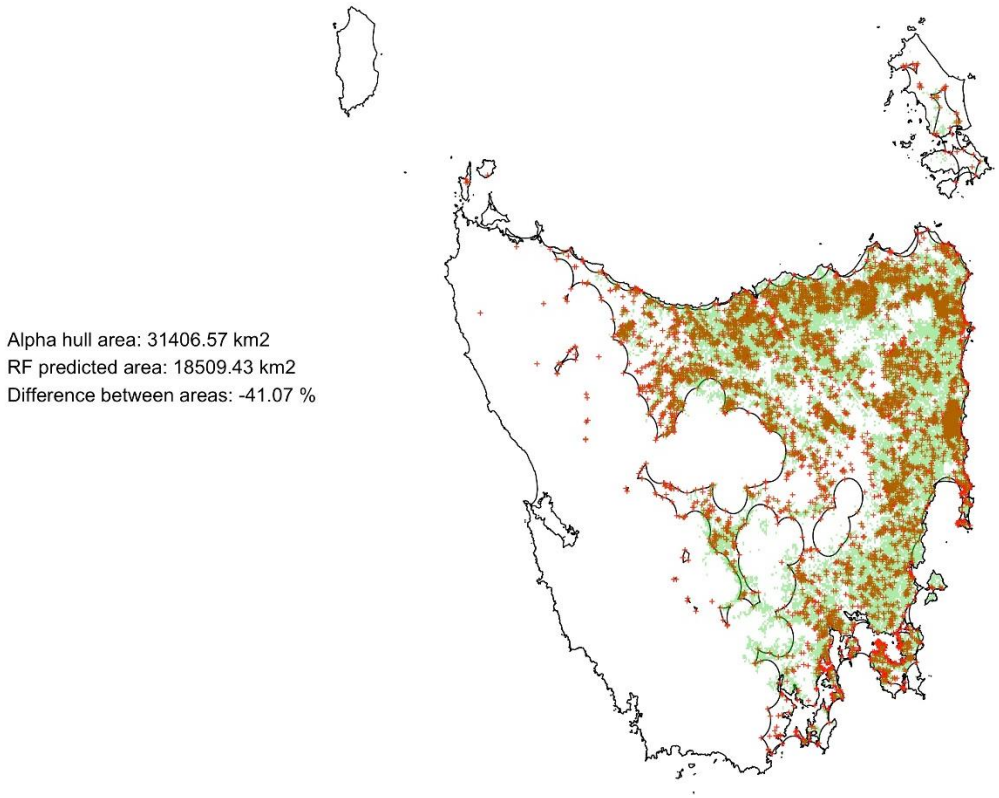
Species	Observations	Random Forest model evaluation				
		m	OOB error	Gini index	Specificity	Sensitivity
Ashes						
Eucalyptus delegatensis	4297	2	0.24	0.54	77.89	86.38
Eucalyptus obliqua	7788	2	0.27	0.56	72.86	85.22
Eucalyptus pauciflora	1069	3	0.20	0.53	80.71	86.88
Eucalyptus regnans	2022	2	0.18	0.53	82.47	89.59
Eucalyptus sieberi	608	7	0.09	0.51	94.29	96.57
Peppermints						
Eucalyptus amygdalina	5826	2	0.29	0.56	72.78	84.46
Eucalyptus coccifera	644	2	0.19	0.51	86.56	89.64
Eucalyptus nebulosa	6	2	0.00	0.50	100.00	100.00
Eucalyptus nitida	1268	3	0.27	0.54	76.50	83.92
Eucalyptus pulchella	1098	3	0.15	0.52	88.57	91.16
Eucalyptus radiata	50	7	0.08	0.50	92.86	93.33
Eucalyptus risdonii	84	3	0.05	0.50	100.00	100.00
Eucalyptus tenuiramis	1009	2	0.18	0.53	85.96	90.94
Black gums						
Eucalyptus barberi	153	7	0.10	0.52	90.91	95.65
Eucalyptus brookeriana	404	7	0.18	0.47	81.2.0	75.00
Eucalyptus ovata	2485	2	0.30	0.58	68.06	82.87
Eucalyptus rodwayi	577	3	0.23	0.49	81.55	79.77
Blue gums						

Eucalyptus globulus	2865	7	0.15	0.54	85.77	79.77
White gums						
Eucalyptus dalrympleana	1348	7	0.21	0.54	81.38	89.60
Eucalyptus rubida	312	7	0.21	0.53	84.44	91.40
Eucalyptus viminalis	5597	7	0.29	0.58	67.49	83.72
Yellow gums						
Eucalyptus johnstonii	204	3	0.13	0.41	91.23	75.41
Eucalyptus subcrenulata	247	2	0.12	0.54	80.00	89.19
Eucalyptus vernicosa	160	3	0.11	0.53	86.96	93.75
Alpine white gums						
Eucalyptus archeri	95	3	0.07	0.48	100.00	96.43
Eucalyptus cordata	86	2	0.10	0.52	91.67	95.83
Eucalyptus gunnii	518	3	0.17	0.54	85.14	92.90
Eucalyptus morrisbyi	5	3	0.20	1.00	100.00	100.00
Eucalyptus perriniana	7	2	0.50	0.50	100.00	100.00
Eucalyptus urnigera	130	7	0.07	0.51	94.74	97.44

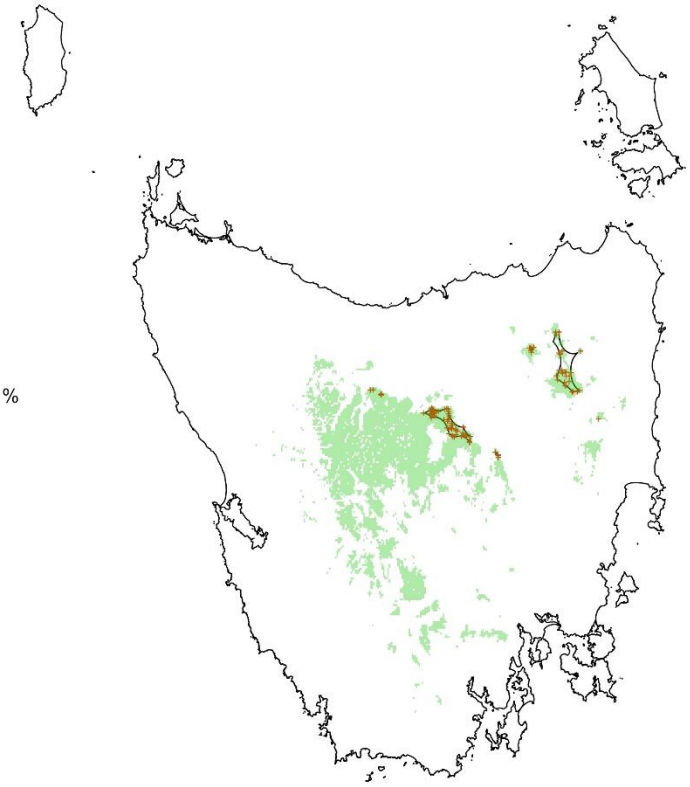
Supplementary material A3

Overprediciton of contemporary suitable habitat by the Random Forest models for the 27 *Eucalyptus* species found in Tasmania. A convex α-hull was created around the occurrence records for each species using the 'ahull' function of the *alphahull* package (Pateiro-López and Rodrıguez-Casal 2010). An $\alpha = 0.1$ was selected as it resulted in realistic polygons that closely matched the distribution of occurrence records (red +). The area of the α-hull and predicted suitable habitat by the Random Forest model (green surface) was calculated using an area raster generated for Tasmania using the 'area' function of the *raster* package. The area raster represents the square-kilometre area of each 30 second grid over Tasmania and adjusts for changes in cell width as distance from the equator increases polewards. Area of predicted and observed area was used to quantify the percentage overprediciton of the distribution of contemporary suitable habitat by the random forest model. Plots of overprediciton have been ordered alphabetical using the species name.

Eucalyptus amygdalina

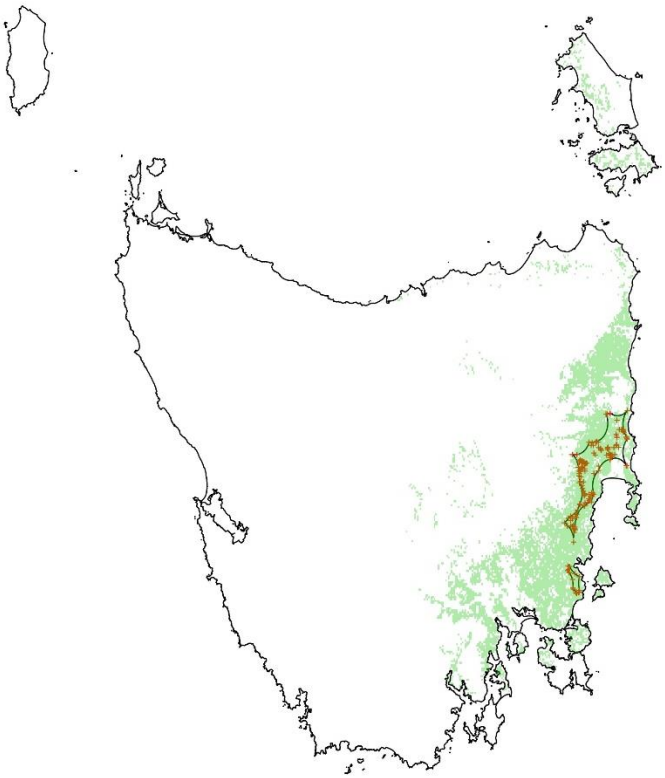


Eucalyptus archeri



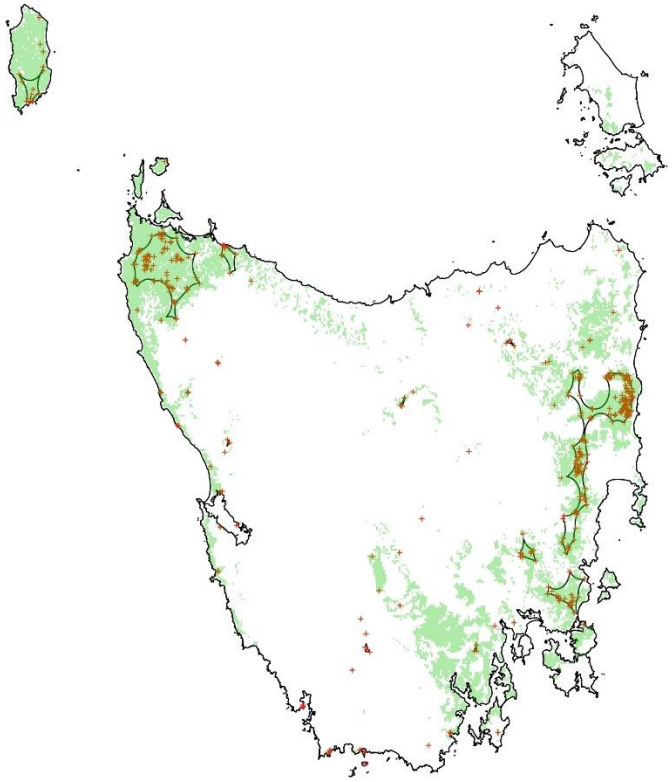
Alpha hull area: 352.11 km2
RF predicted area: 5939.88 km2
Difference between areas: 1586.94 %

Eucalyptus barberi



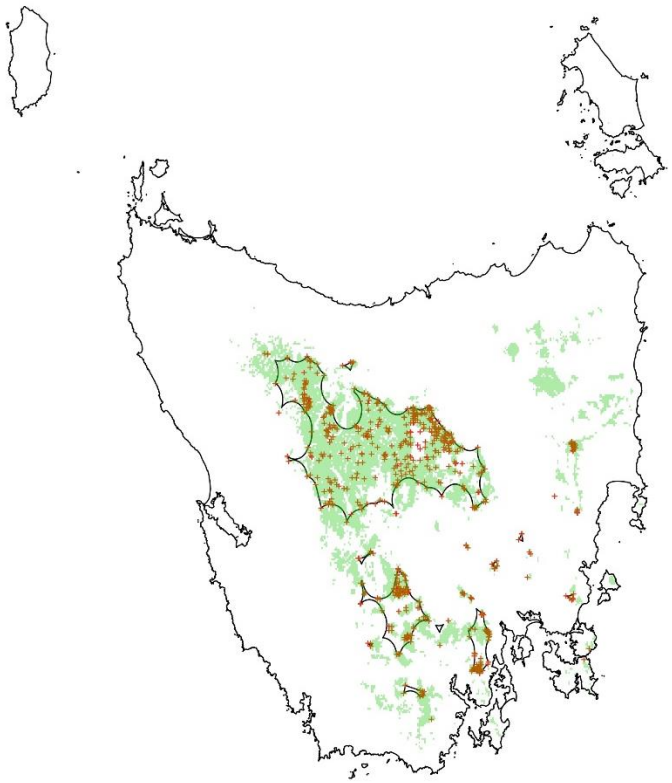
Alpha hull area: 791.05 km2
RF predicted area: 6256.88 km2
Difference between areas: 690.95 %

Eucalyptus brookeriana



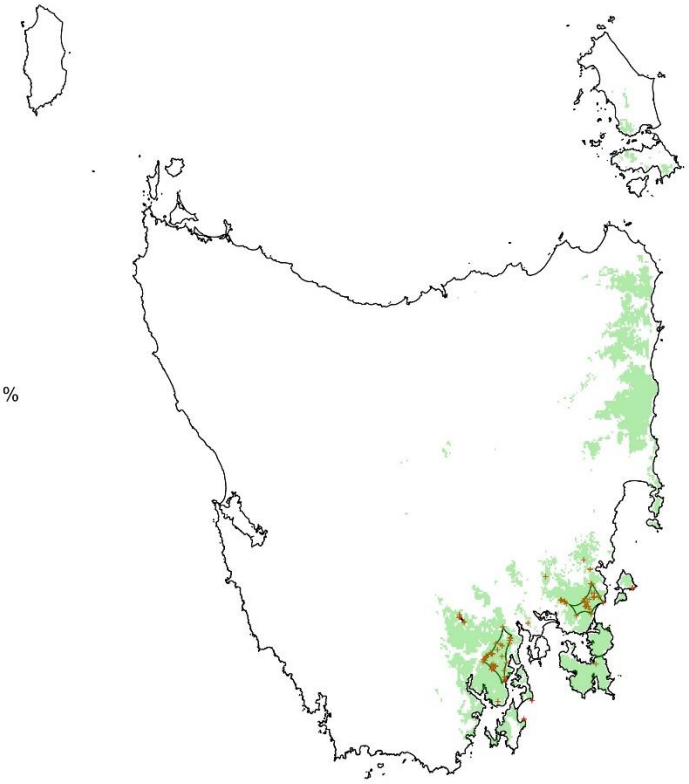
Alpha hull area: 2281.62 km2
RF predicted area: 11256.54 km2
Difference between areas: 393.36 %

Eucalyptus coccifera



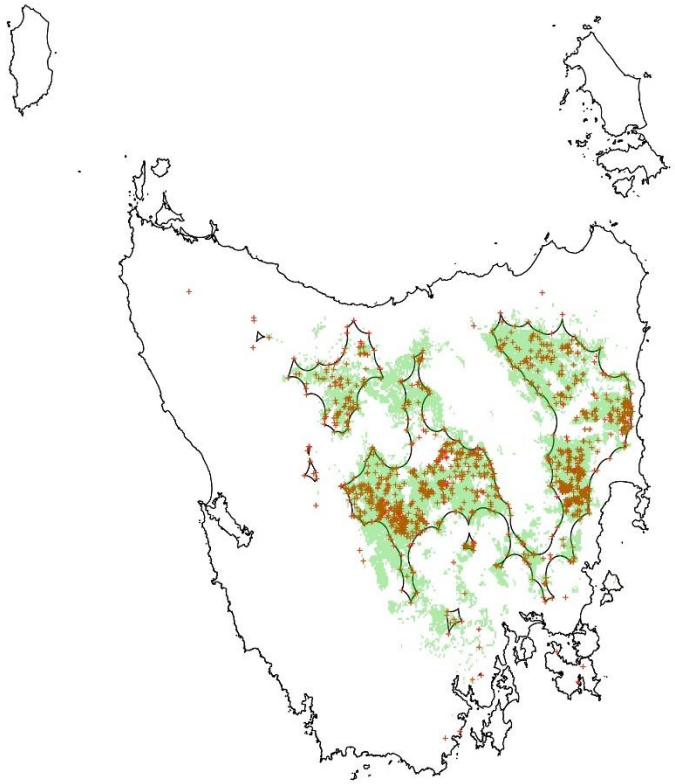
Alpha hull area: 6378.94 km2
RF predicted area: 8540.81 km2
Difference between areas: 33.89 %

Eucalyptus cordata



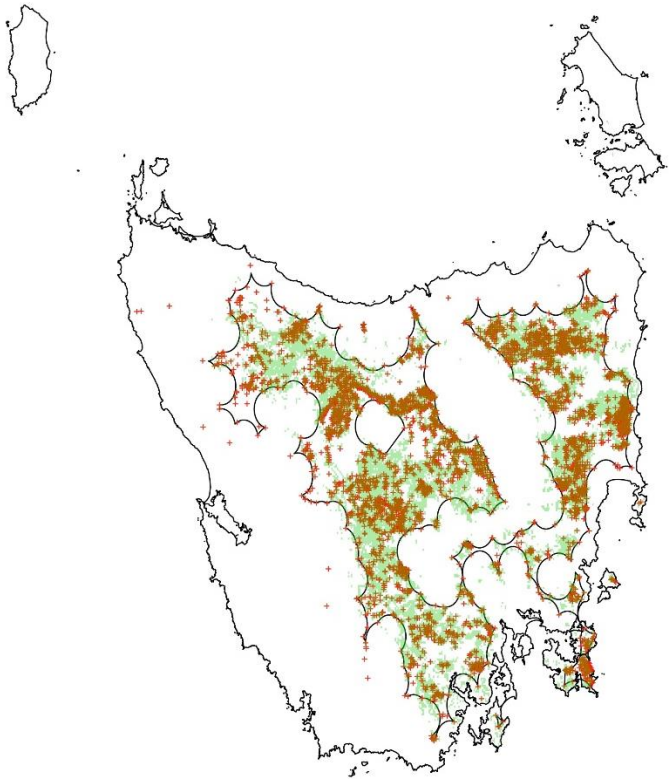
Alpha hull area: 353.97 km2
RF predicted area: 5411.66 km2
Difference between areas: 1428.86 %

Eucalyptus dalrympleana



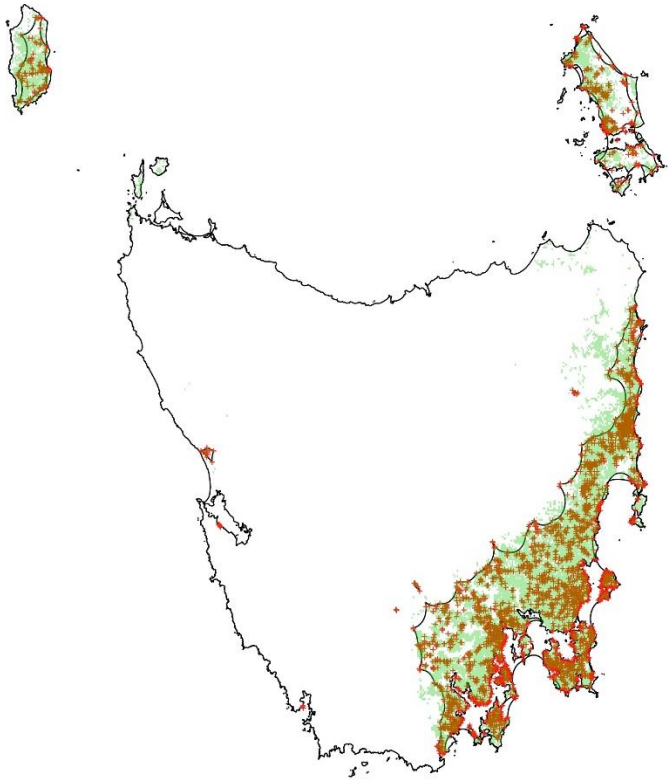
Alpha hull area: 10868.55 km2
RF predicted area: 11444.83 km2
Difference between areas: 5.3 %

Eucalyptus delegatensis



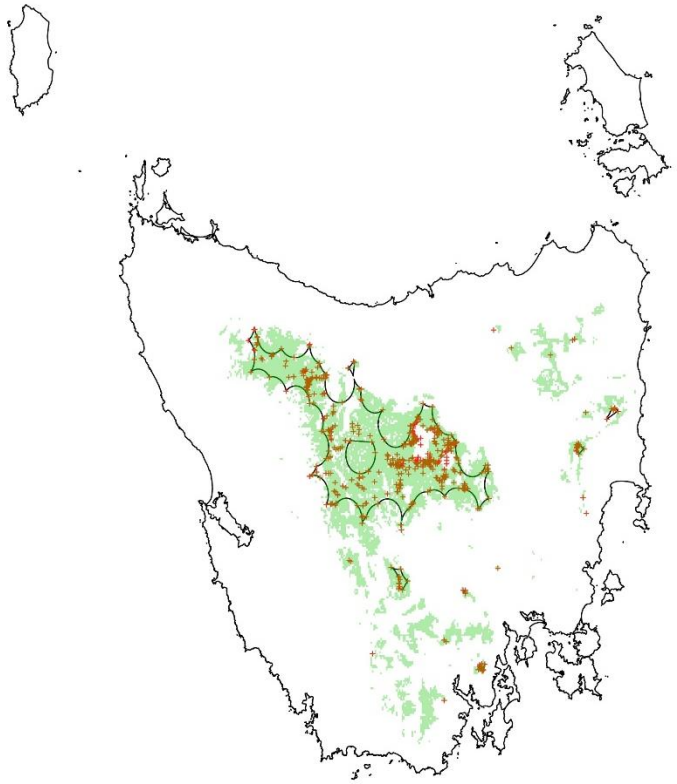
Alpha hull area: 22190.16 km2
RF predicted area: 14024.32 km2
Difference between areas: -36.8 %

Eucalyptus globulus



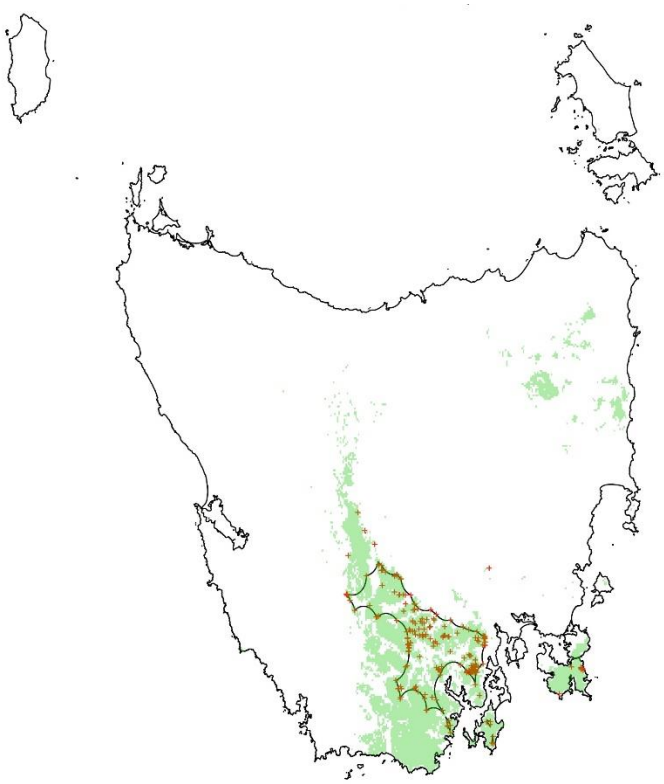
Alpha hull area: 13143.52 km2
RF predicted area: 10015.26 km2
Difference between areas: -23.8 %

Eucalyptus gunnii



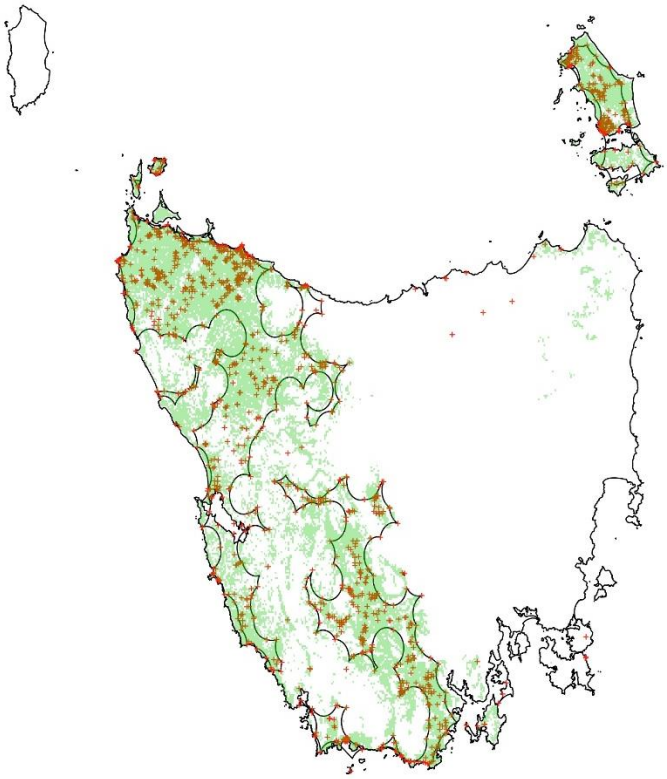
Alpha hull area: 4632.56 km2
RF predicted area: 8753.2 km2
Difference between areas: 88.95 %

Eucalyptus johnstonii



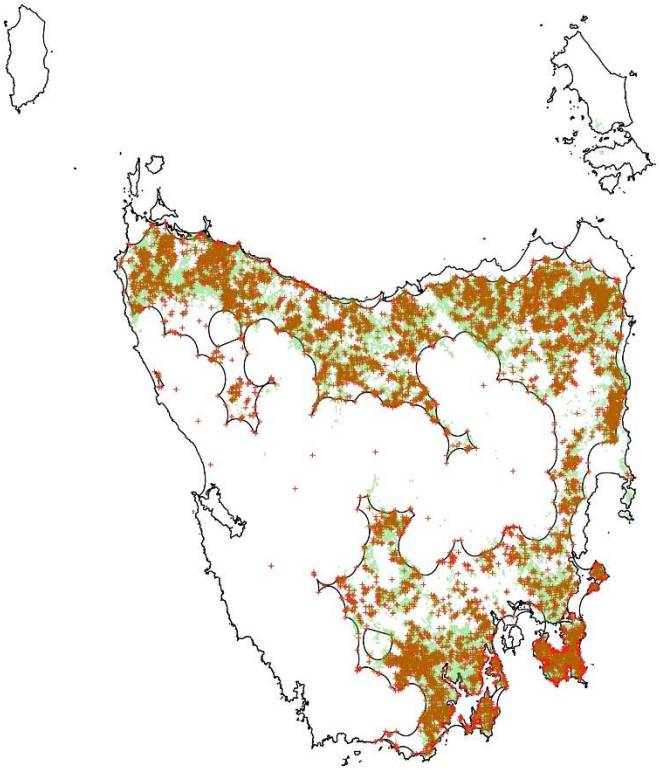
Alpha hull area: 2380.51 km2
RF predicted area: 6106.58 km2
Difference between areas: 156.52 %

Eucalyptus nitida



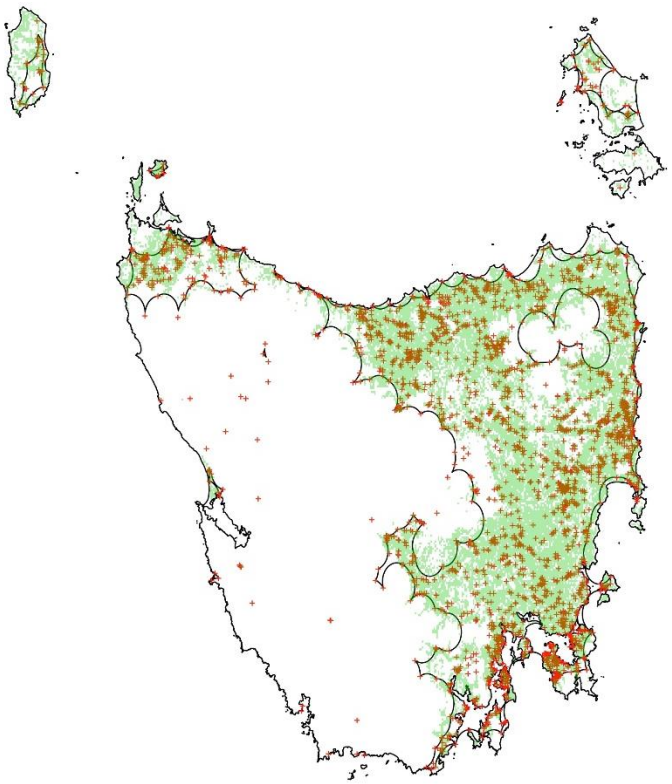
Alpha hull area: 15317.27 km2
RF predicted area: 16996.61 km2
Difference between areas: 10.96 %

Eucalyptus obliqua



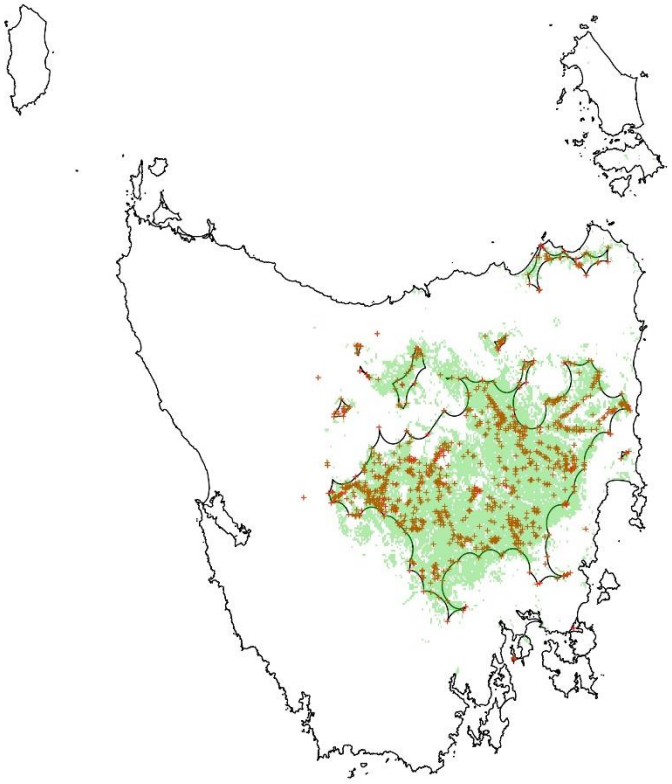
Alpha hull area: 30655.1 km2
RF predicted area: 17302.86 km2
Difference between areas: -43.56 %

Eucalyptus ovata



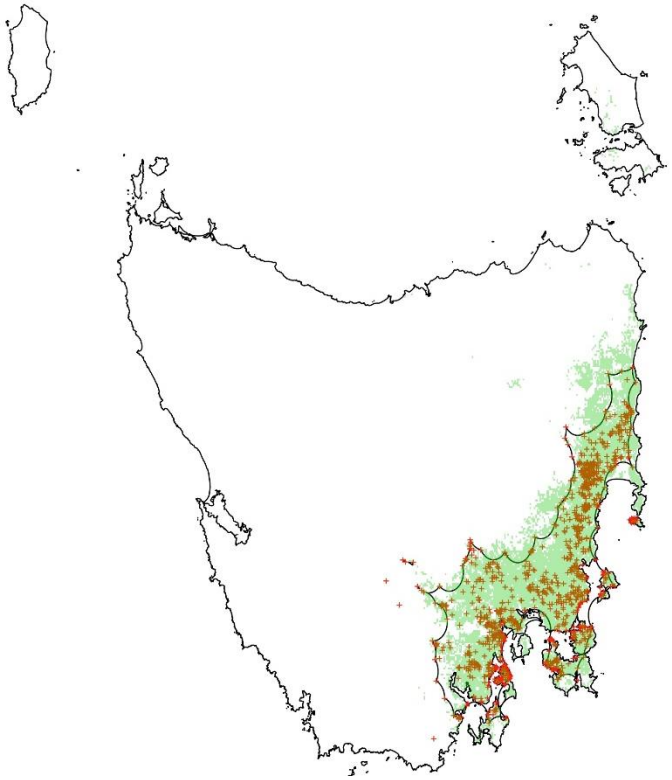
Alpha hull area: 28435.49 km2
RF predicted area: 21186.78 km2
Difference between areas: -25.49 %

Eucalyptus pauciflora



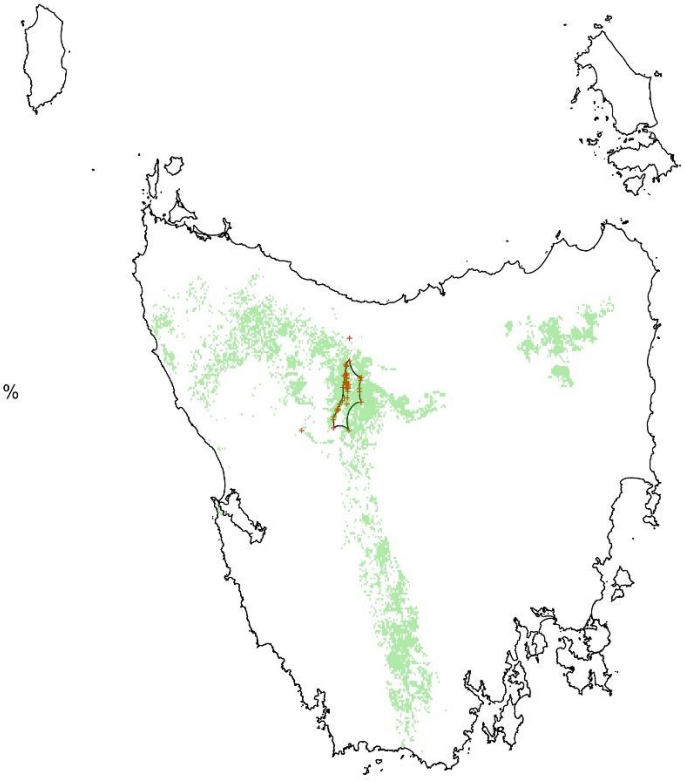
Alpha hull area: 11537.24 km2
RF predicted area: 12837.47 km2
Difference between areas: 11.27 %

Eucalyptus pulchella



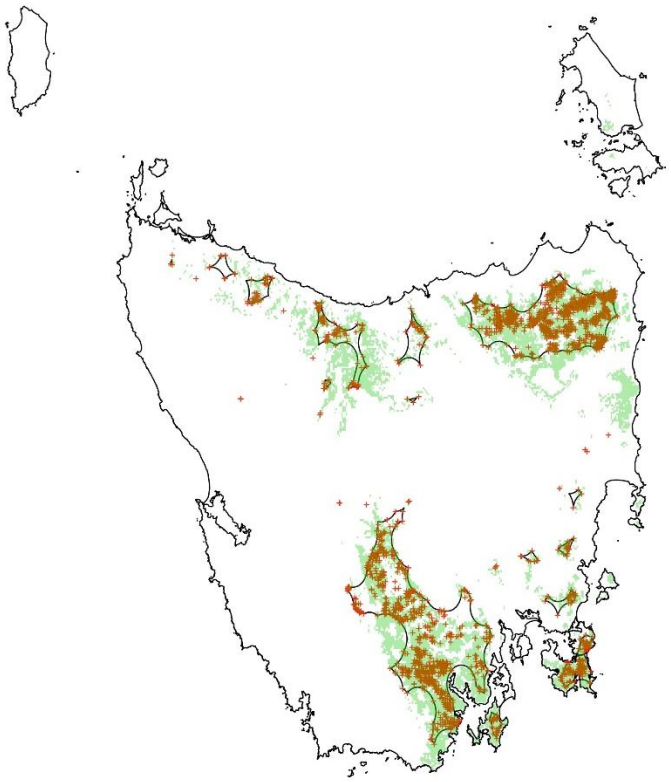
Alpha hull area: 8275.88 km2
RF predicted area: 8459.19 km2
Difference between areas: 2.21 %

Eucalyptus radiata



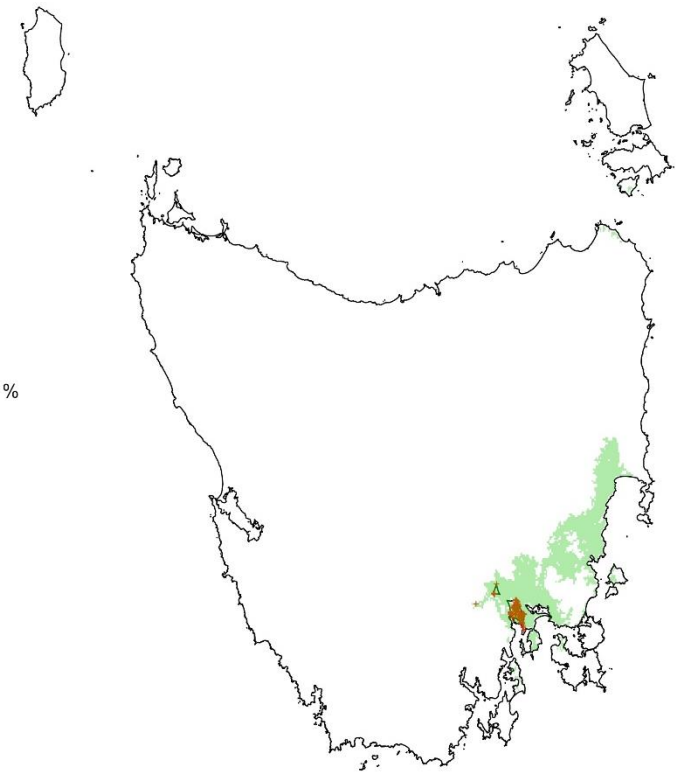
Alpha hull area: 307.6 km2
RF predicted area: 5074.26 km2
Difference between areas: 1549.63 %

Eucalyptus regnans



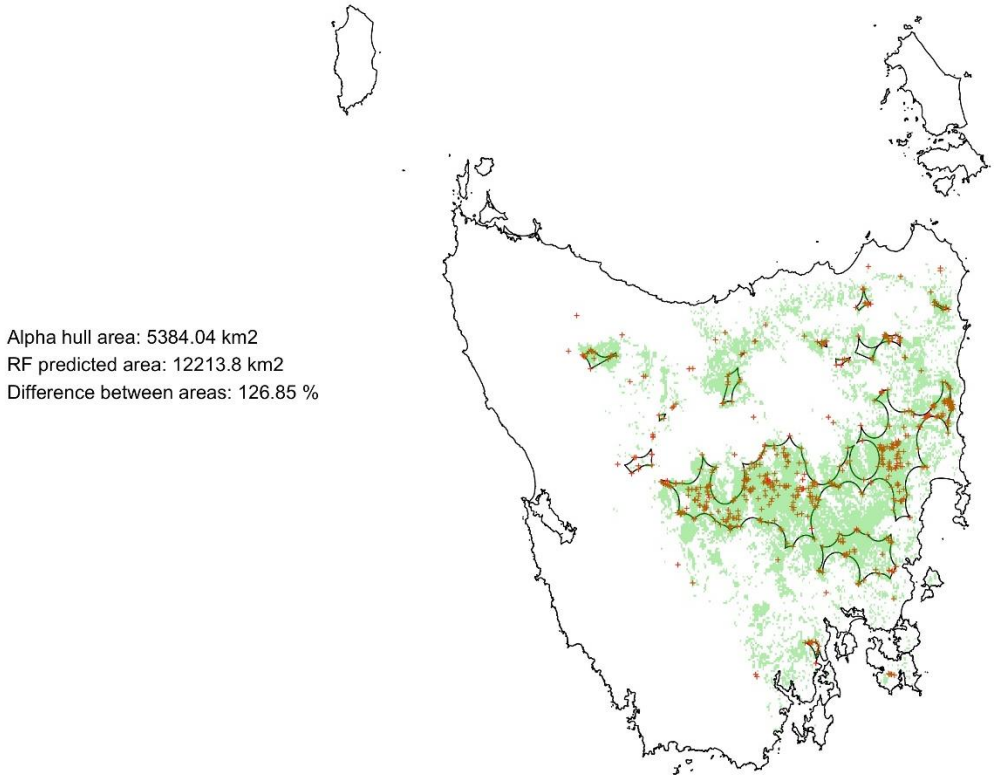
Alpha hull area: 7618.11 km2
RF predicted area: 9950.82 km2
Difference between areas: 30.62 %

Eucalyptus risdonii

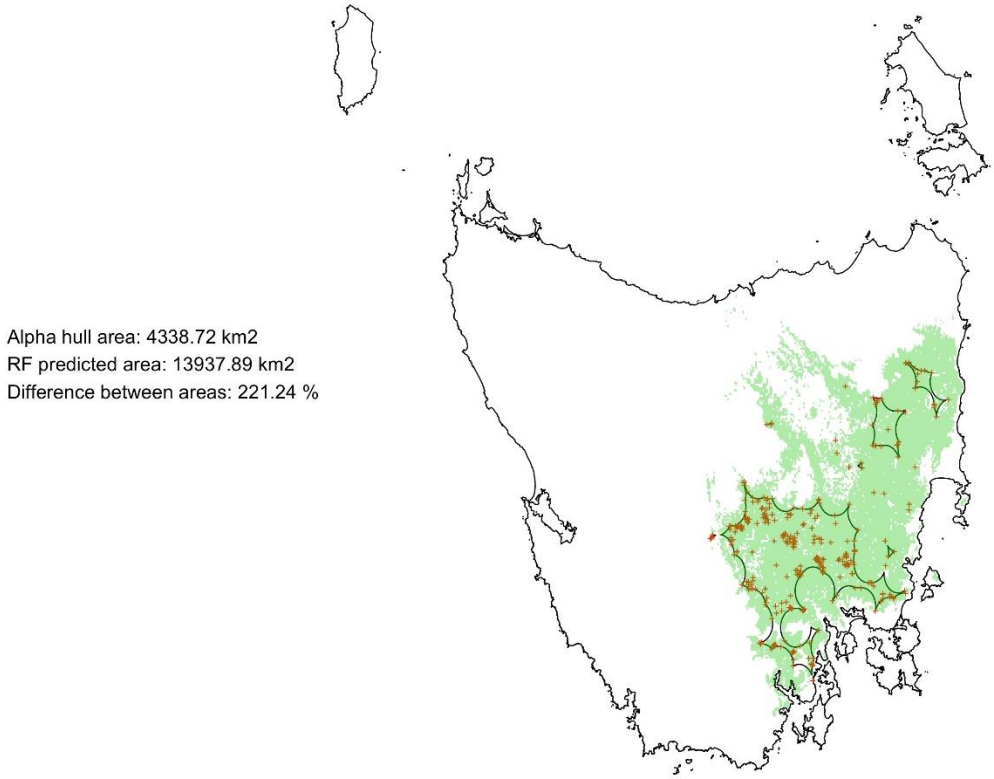


Alpha hull area: 85.03 km2
RF predicted area: 2614.9 km2
Difference between areas: 2975.45 %

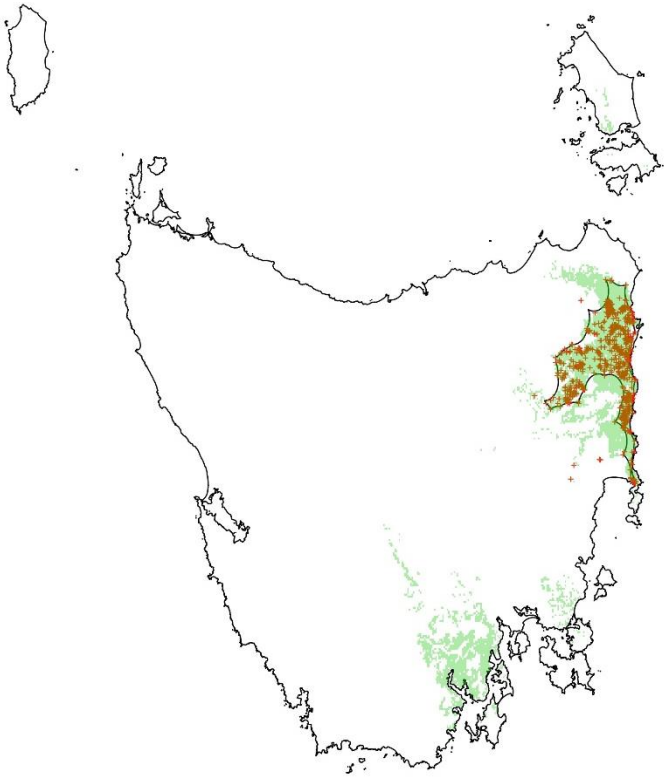
Eucalyptus rodwayi



Eucalyptus rubida

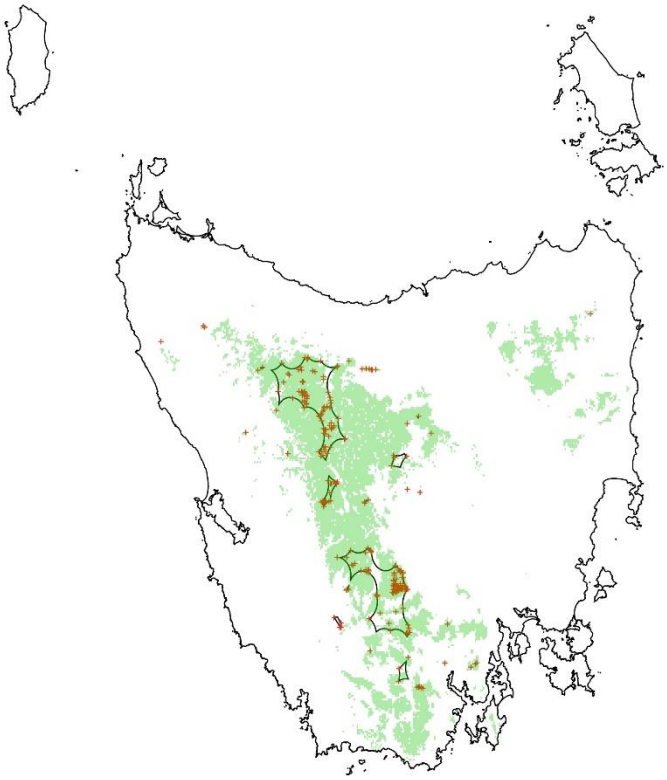


Eucalyptus sieberi



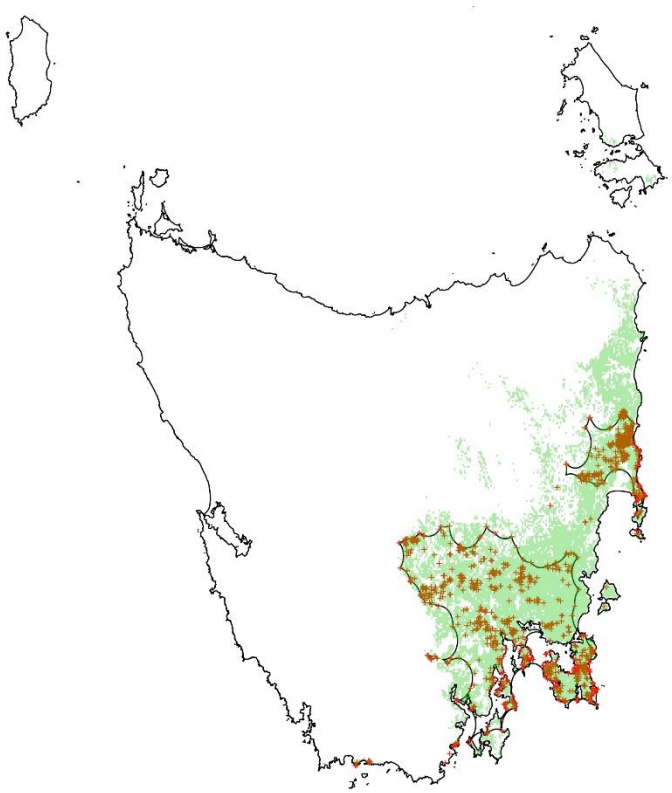
Alpha hull area: 2133.93 km2
RF predicted area: 4428 km2
Difference between areas: 107.5 %

Eucalyptus subcrenulata



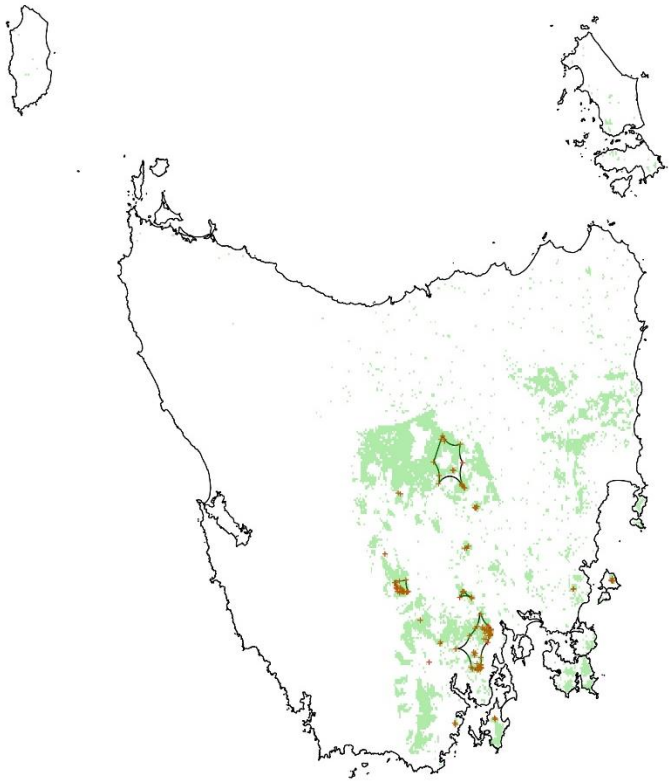
Alpha hull area: 1931.93 km2
RF predicted area: 10358.79 km2
Difference between areas: 436.19 %

Eucalyptus tenuiramis



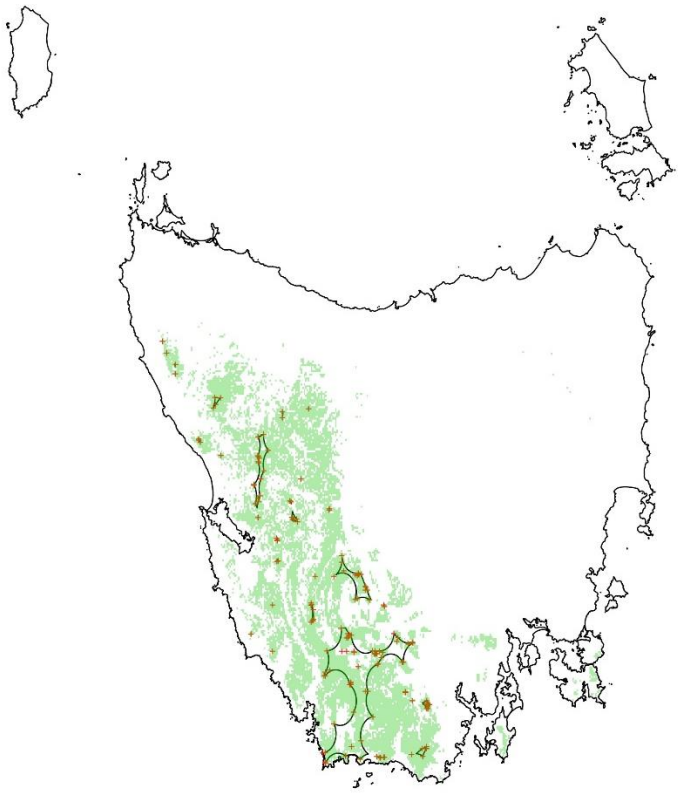
Alpha hull area: 8447.76 km2
RF predicted area: 10225.81 km2
Difference between areas: 21.05 %

Eucalyptus unigera



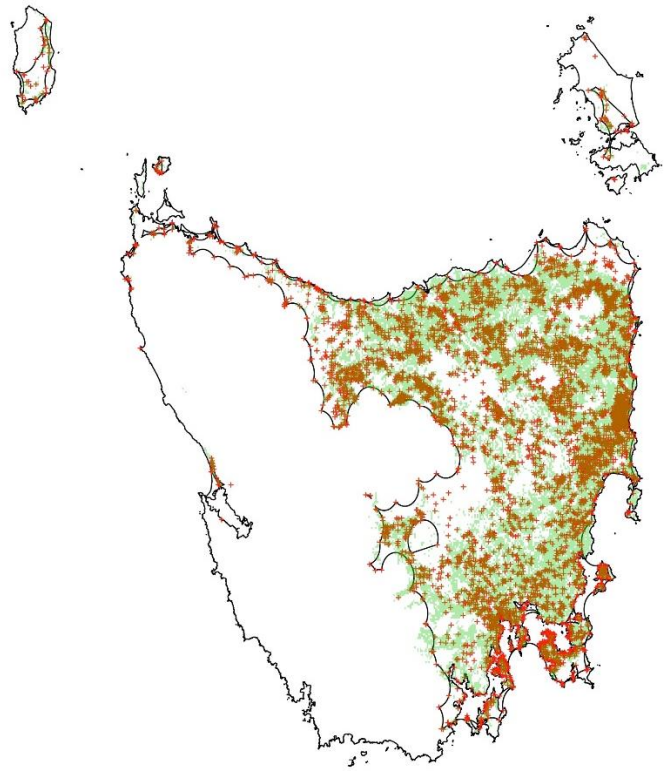
Alpha hull area: 604.72 km2
RF predicted area: 5971.86 km2
Difference between areas: 887.54 %

Eucalyptus vernicosa



Alpha hull area: 1416.57 km2
RF predicted area: 10216.67 km2
Difference between areas: 621.22 %

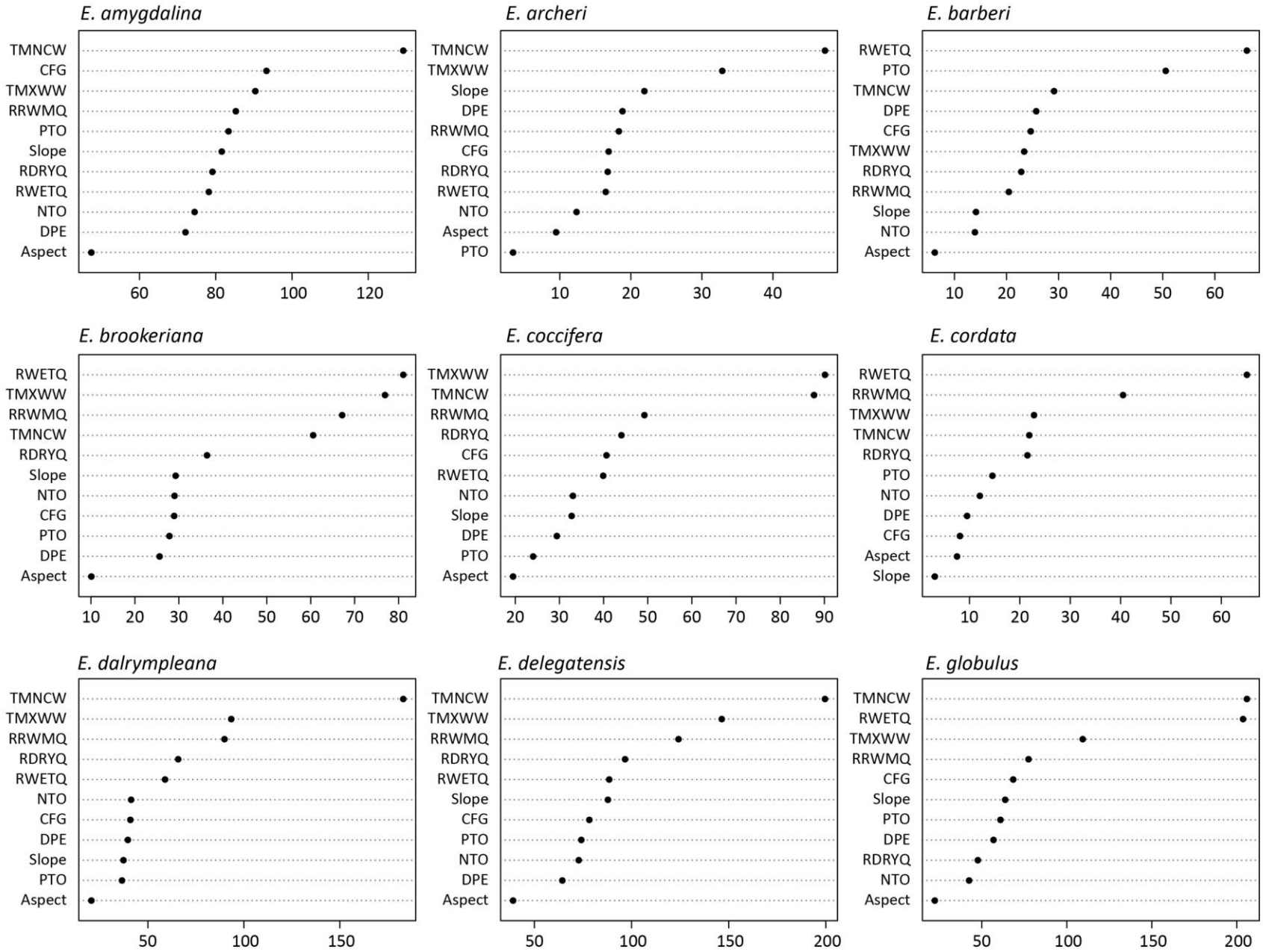
Eucalyptus viminalis

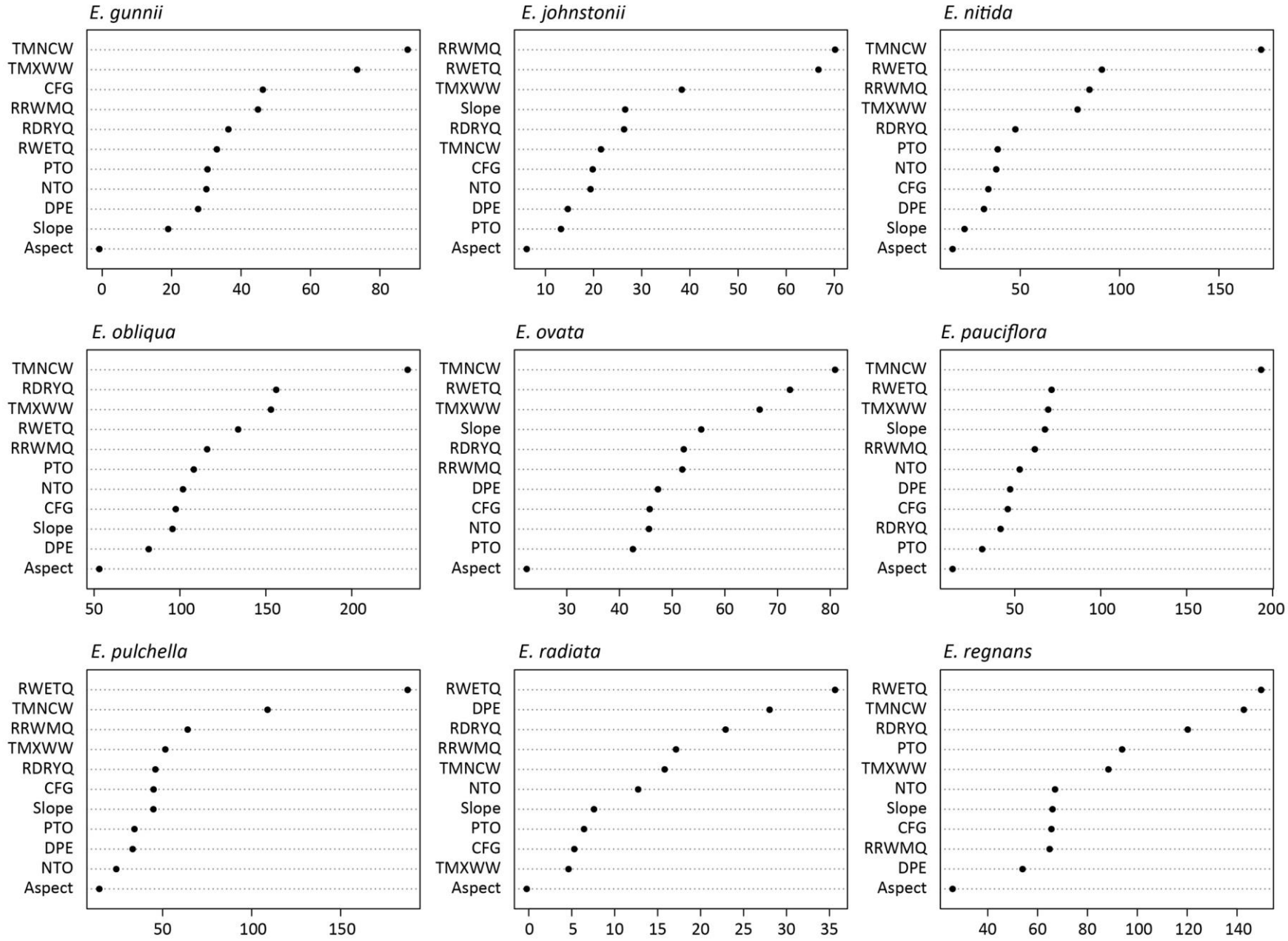


Alpha hull area: 33702.09 km2
RF predicted area: 19719.62 km2
Difference between areas: -41.49 %

Supplementary material A4

The importance of each predictor variable in the Random Forest used to model the extent of suitable habitat for each of the 27 *Eucalyptus* species. Shown is the importance of each variable (y-axis) based on the percentage increase in mean squared error (x-axis) that was estimated using the out-of-bag (OOB) samples, after randomly permutating the OOB data for a predictor whilst leaving all others unchanged. Here, high values of percentage increase in mean squared error suggests that the varaible is most important in the classification model. Species have been ordered alphabetical, and the varaibles for each species have been ordered by their increase in mean squared error. (Abbreviations: maximum temperature of the warmest week (TMXWW), minimum temperature of the coldest week (TMNCW), precipitation of the driest quarter (RWETQ), precipiation of the wettest quarter (RWETQ), radiation of the warmest quarter (RRWMQ), percent total nitrogen (NTO), percent total phosphorous (PTO), plant exploitable depth (DPE), coarse fragments > 2 mm (CFG), slope, aspect).


E. amygdalina
TMNCW
CFG
TMXWW
RRWMQ
PTO
Slope
RDRYQ
RWETQ
NTO
DPE
Aspect
60
80
100
120
E. archeri
TMNCW
TMXWW
Slope
DPE
RRWMQ
CFG
RDRYQ
RWETQ
NTO
Aspect
PTO
10
20
30
40
E. barberi
RWETQ
PTO
TMNCW
DPE
CFG
TMXWW
RDRYQ
RRWMQ
Slope
NTO
Aspect
10
20
30
40
50
60
E. brookeriana
RWETQ
TMXWW
RRWMQ
TMNCW
RDRYQ
Slope
NTO
CFG
PTO
DPE
Aspect
10
20
30
40
50
60
70
80
E. coccifera
TMXWW
TMNCW
RRWMQ
RDRYQ
CFG
RWETQ
NTO
Slope
DPE
PTO
Aspect
20
30
40
50
60
70
80
90
E. cordata
RWETQ
RRWMQ
TMXWW
TMNCW
RDRYQ
PTO
NTO
DPE
CFG
Aspect
Slope
10
20
30
40
50
60
E. dalrympleana
TMNCW
TMXWW
RRWMQ
RDRYQ
RWETQ
NTO
CFG
DPE
Slope
PTO
Aspect
50
100
150
E. delegatensis
TMNCW
TMXWW
RRWMQ
RDRYQ
RWETQ
Slope
CFG
PTO
NTO
DPE
Aspect
50
100
150
200
E. globulus
TMNCW
RWETQ
TMXWW
RRWMQ
CFG
Slope
PTO
DPE
RDRYQ
NTO
Aspect
50
100
150
200


E. gunnii
TMNCW
TMXWW
CFG
RRWMQ
RDRYQ
RWETQ
PTO
NTO
DPE
Slope
Aspect
0 20 40 60 80
E. johnstonii
RRWMQ
RWETQ
TMXWW
Slope
RDRYQ
TMNCW
CFG
NTO
DPE
PTO
Aspect
10 20 30 40 50 60 70
E. nitida
TMNCW
RWETQ
RRWMQ
TMXWW
RDRYQ
PTO
NTO
CFG
DPE
Slope
Aspect
50 100 150
E. obliqua
TMNCW
RDRYQ
TMXWW
RWETQ
RRWMQ
PTO
NTO
CFG
Slope
DPE
Aspect
50 100 150 200
E. ovata
TMNCW
RWETQ
TMXWW
Slope
RDRYQ
RRWMQ
DPE
CFG
NTO
PTO
Aspect
30 40 50 60 70 80
E. pauciflora
TMNCW
RWETQ
TMXWW
Slope
RRWMQ
NTO
DPE
CFG
RDRYQ
PTO
Aspect
50 100 150 200
E. pulchella
RWETQ
TMNCW
RRWMQ
TMXWW
RDRYQ
CFG
Slope
PTO
DPE
NTO
Aspect
50 100 150
E. radiata
RWETQ
DPE
RDRYQ
RRWMQ
TMNCW
NTO
Slope
PTO
CFG
TMXWW
Aspect
0 5 10 15 20 25 30 35
E. regnans
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RDRYQ
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NTO
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RRWMQ
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Aspect
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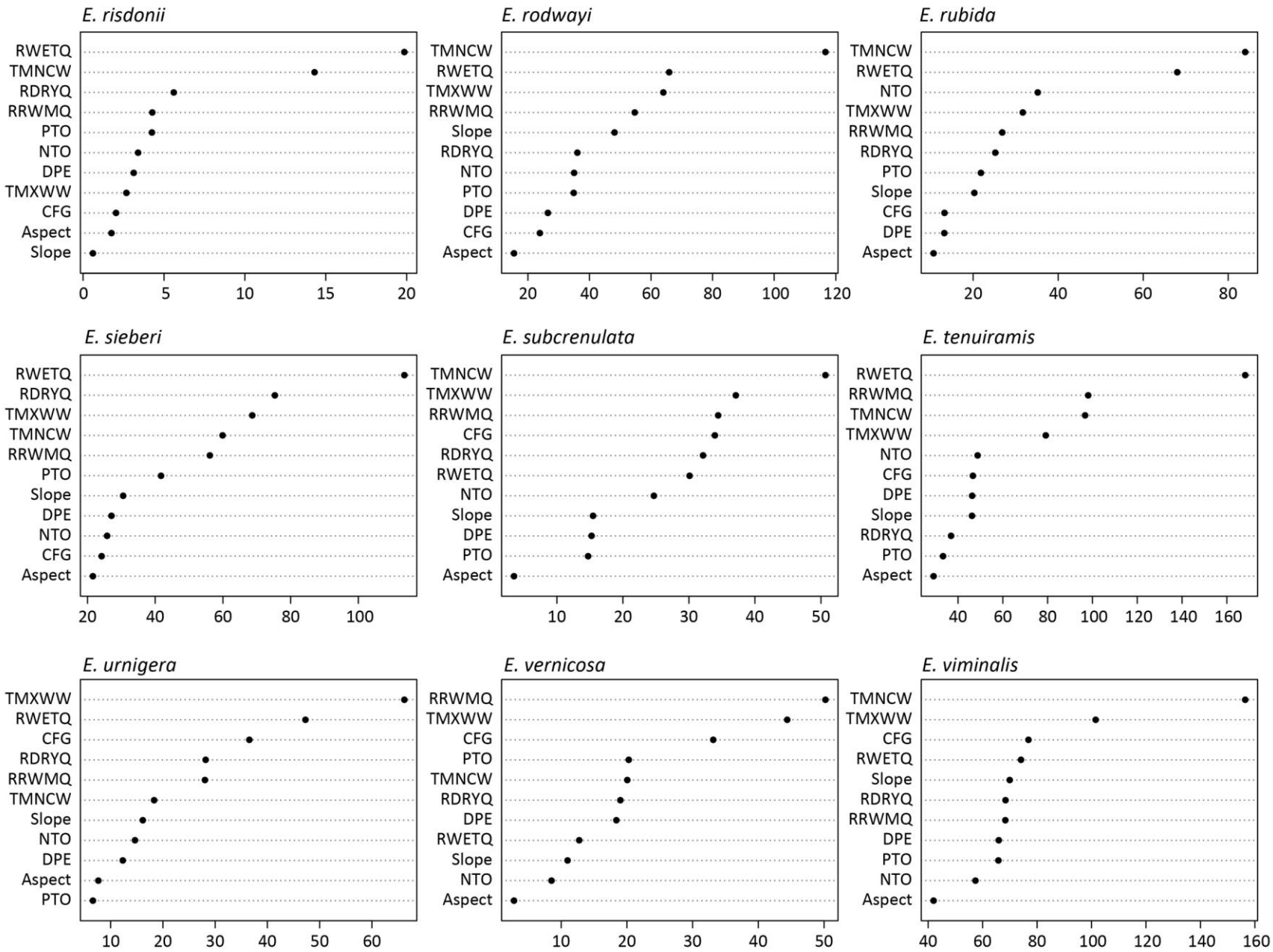
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E. rodwayi
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RWETQ
TMXWW
RRWMQ
Slope
RDRYQ
NTO
PTO
DPE
CFG
Aspect
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RWETQ
NTO
TMXWW
RRWMQ
RDRYQ
PTO
Slope
CFG
DPE
Aspect
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E. sieberi
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RDRYQ
TMXWW
TMNCW
RRWMQ
PTO
Slope
DPE
NTO
CFG
Aspect
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E. subcrenulata
TMNCW
TMXWW
RRWMQ
CFG
RDRYQ
RWETQ
NTO
Slope
DPE
PTO
Aspect
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RRWMQ
TMNCW
TMXWW
NTO
CFG
DPE
Slope
RDRYQ
PTO
Aspect
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CFG
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Slope
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DPE
Aspect
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RRWMQ
TMXWW
CFG
PTO
TMNCW
RDRYQ
DPE
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Slope
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Aspect
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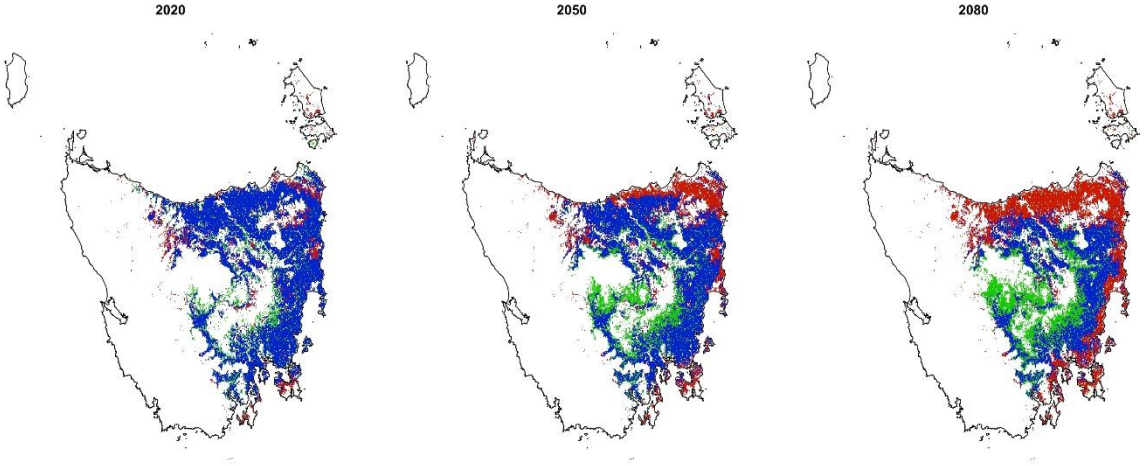
E. viminalis
TMNCW
TMXWW
CFG
RWETQ
Slope
RDRYQ
RRWMQ
DPE
PTO
NTO
Aspect
40 60 80 100 120 140 160

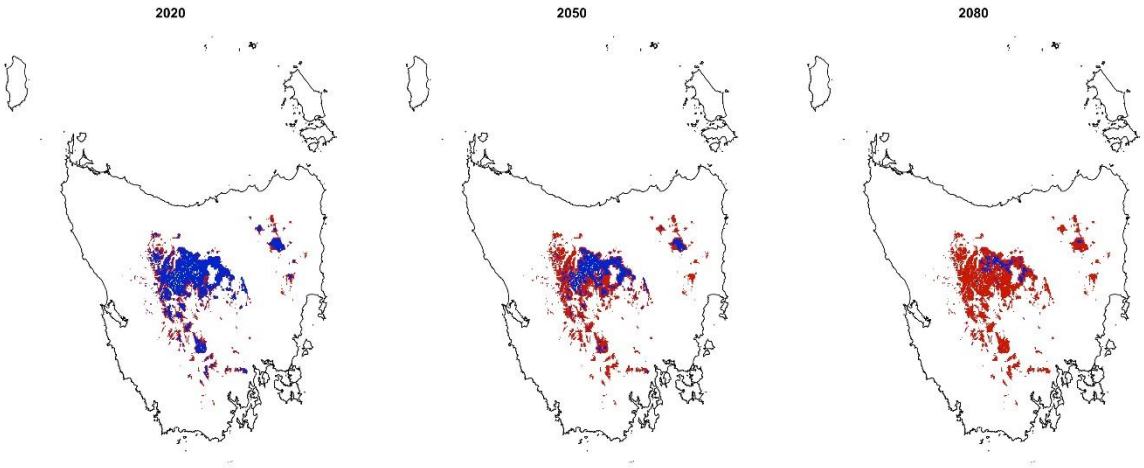
Supplementary material A5

Spatiotemporal change in the modelled suitable habitat for each species under climate change. The expansion (green), extirpation (red), and stability (blue) of modelled suitable habitat was calculated by subtracting the contemporary distribution of modelled suitable habitat from the predicated distribution of suitable habitat for the future climate of the 2020s (left-hand side), 2050s (middle), and 2080s (right-hand side).

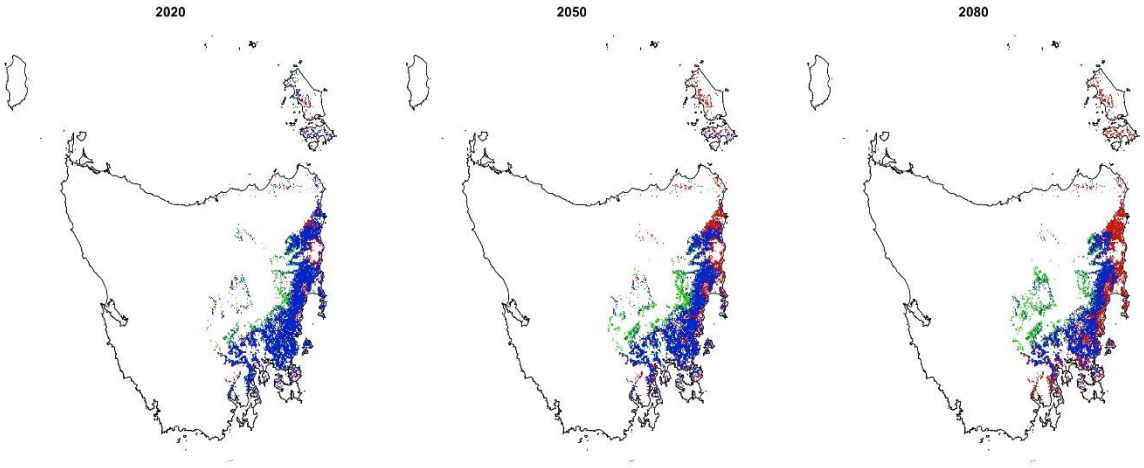
Eucalyptus amygdalina



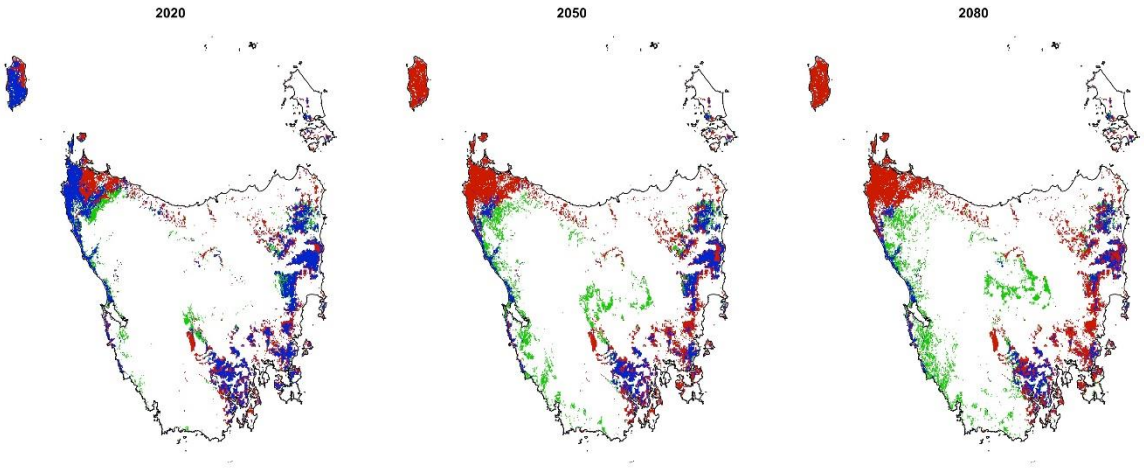
Eucalyptus archeri



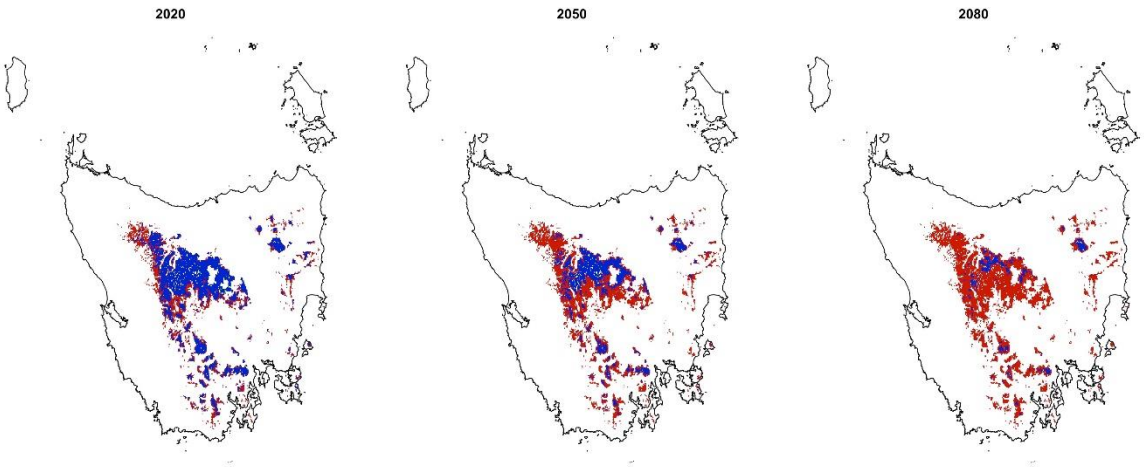
Eucalyptus barberi



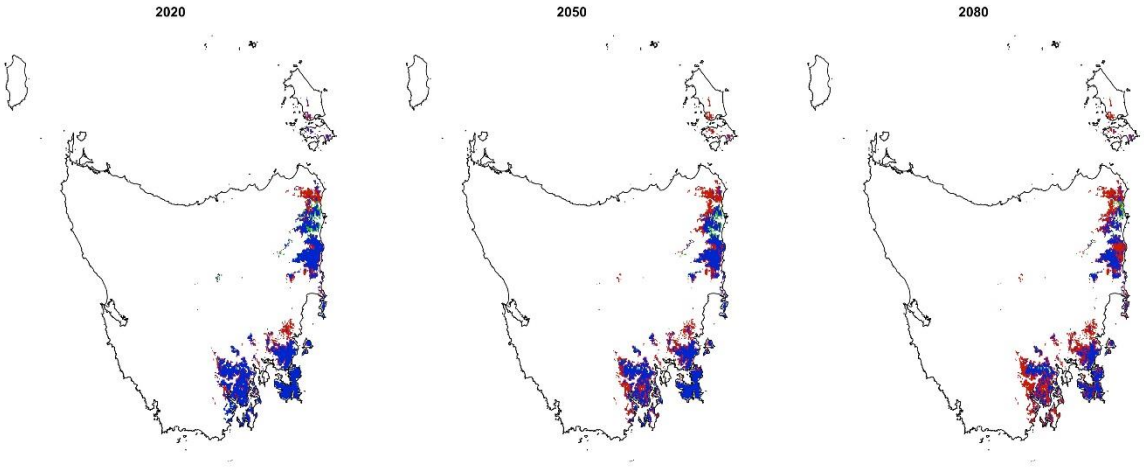
Eucalyptus brookeriana



Eucalyptus coccifera



Eucalyptus cordata



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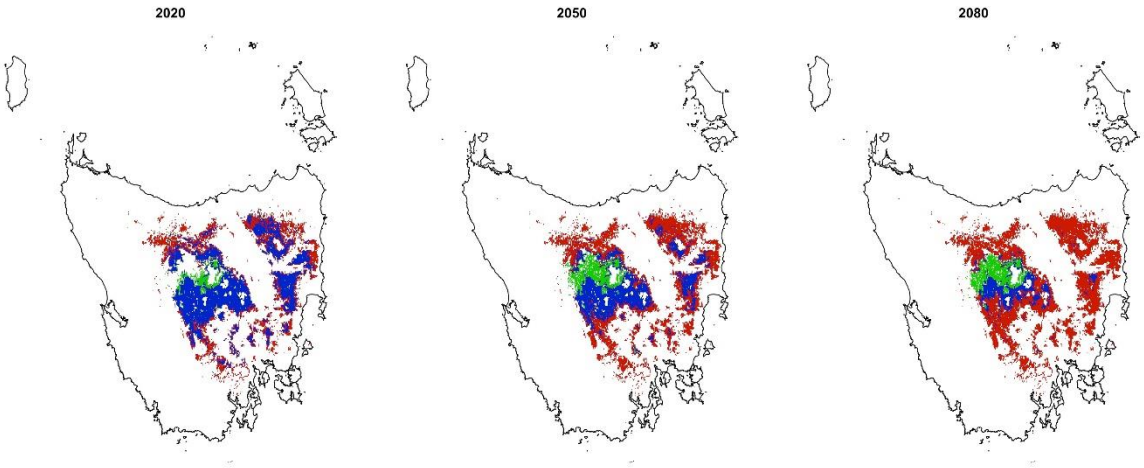

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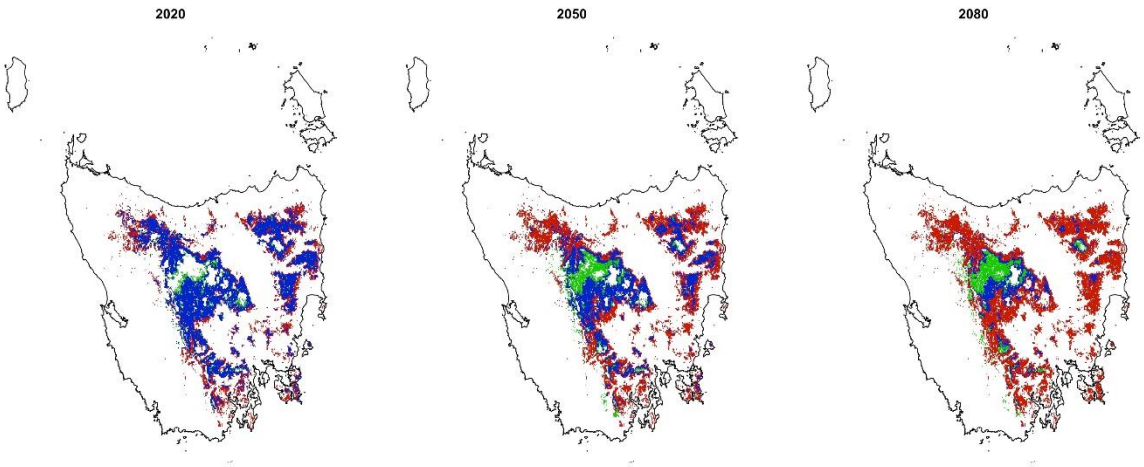
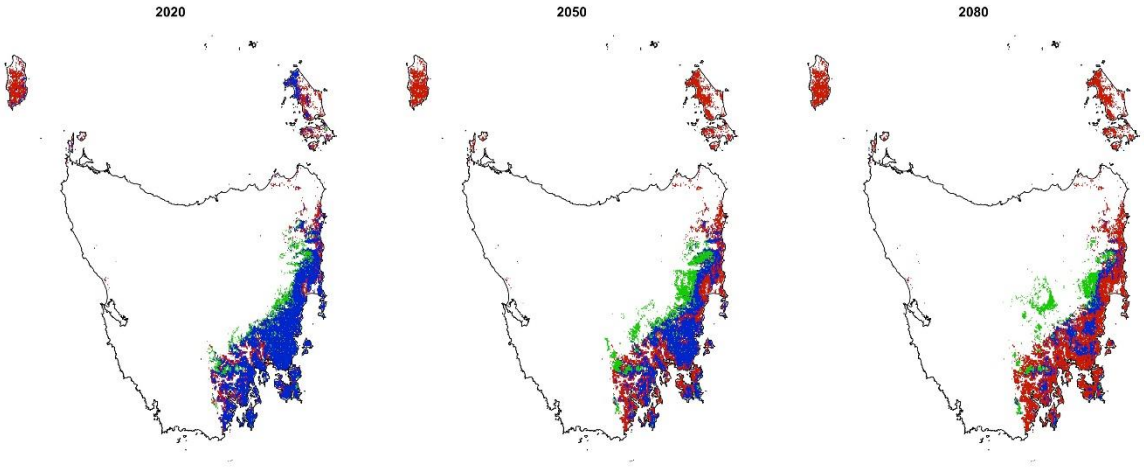
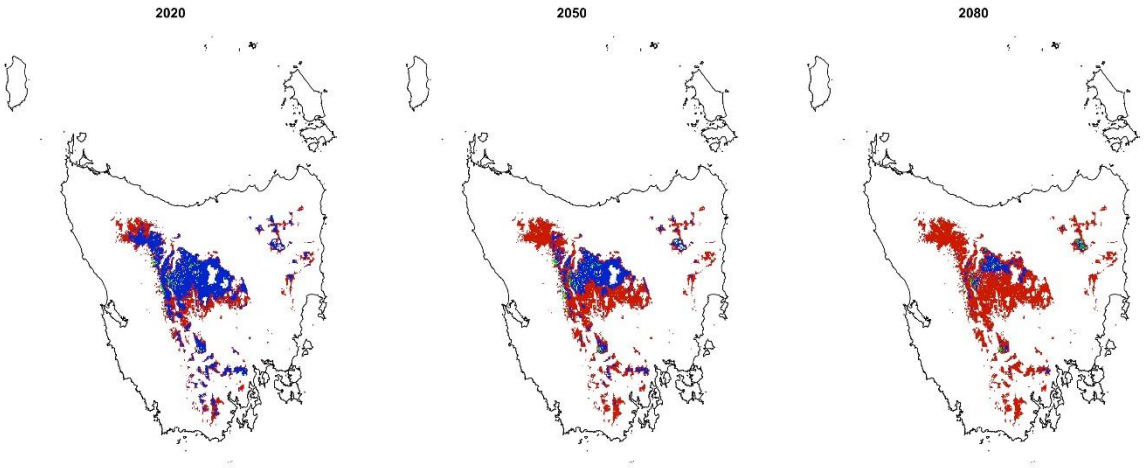


Eucalyptus globulus



Eucalyptus gunnii



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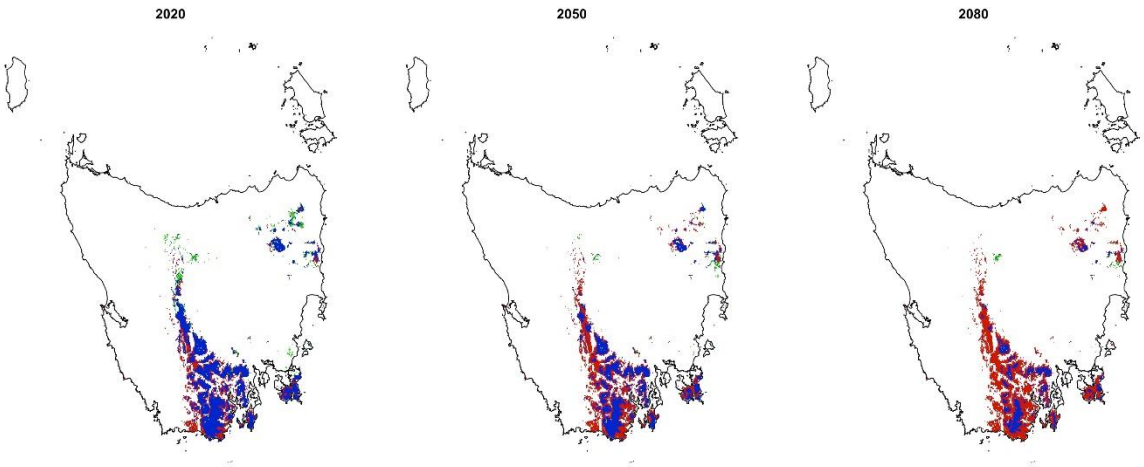

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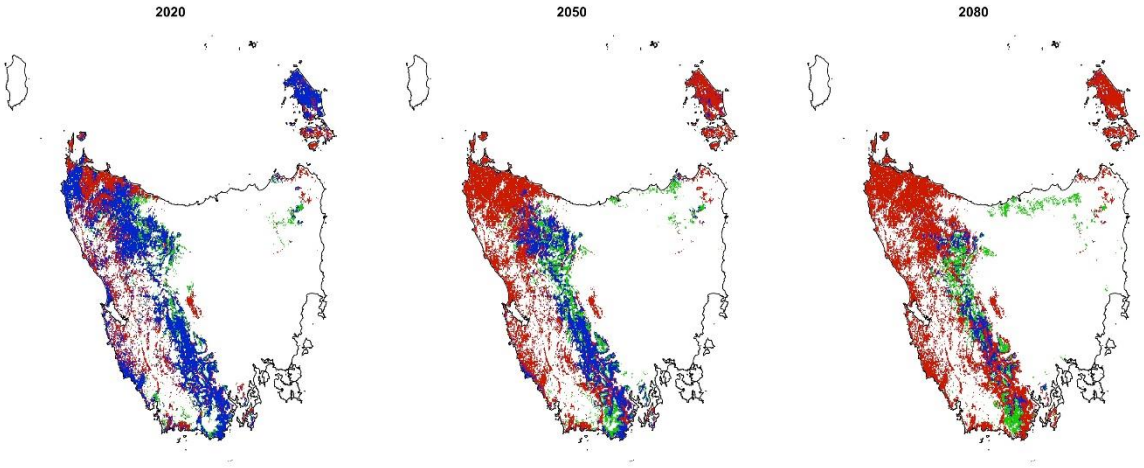

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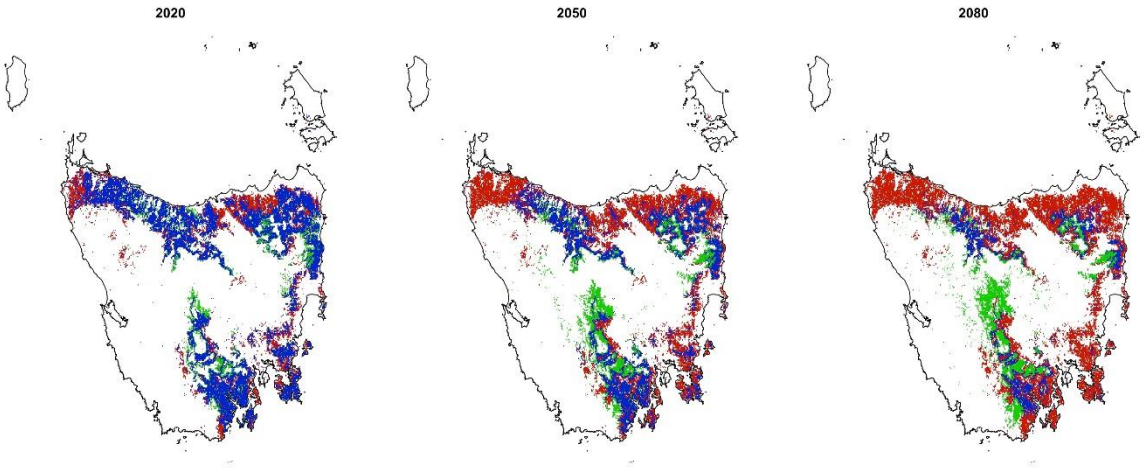
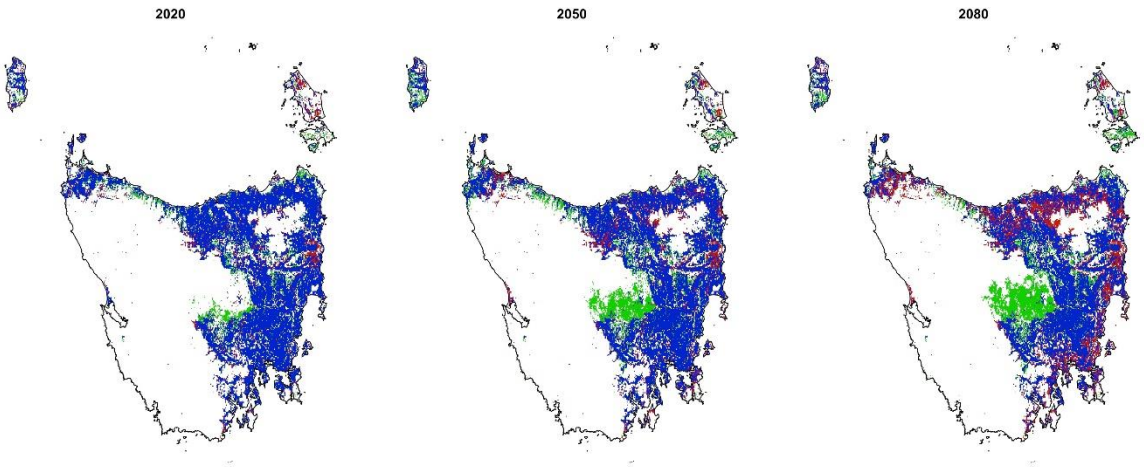
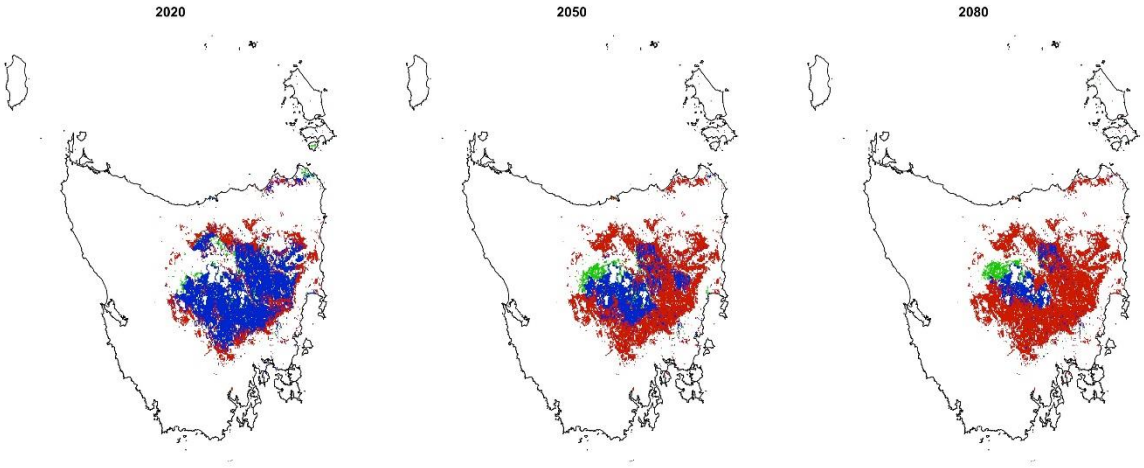


Eucalyptus ovata



Eucalyptus pauciflora



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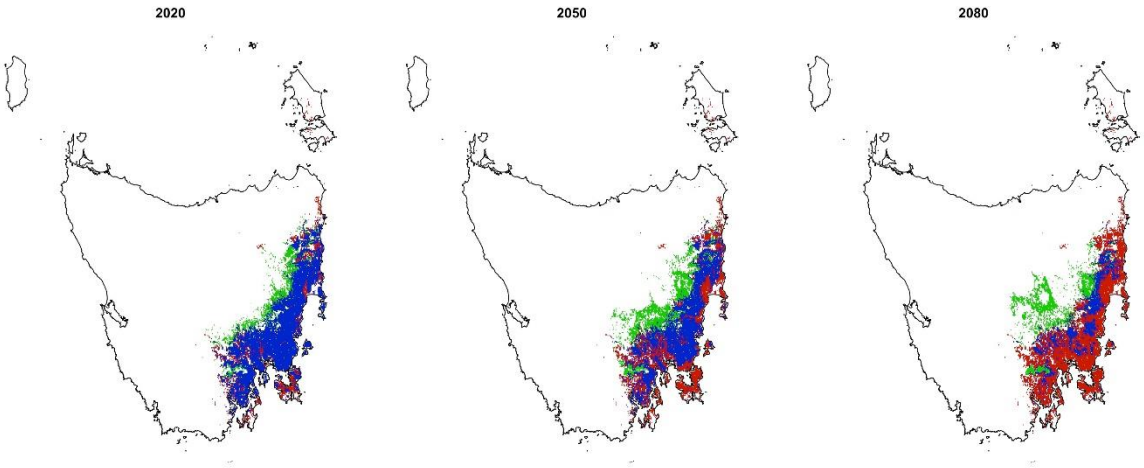

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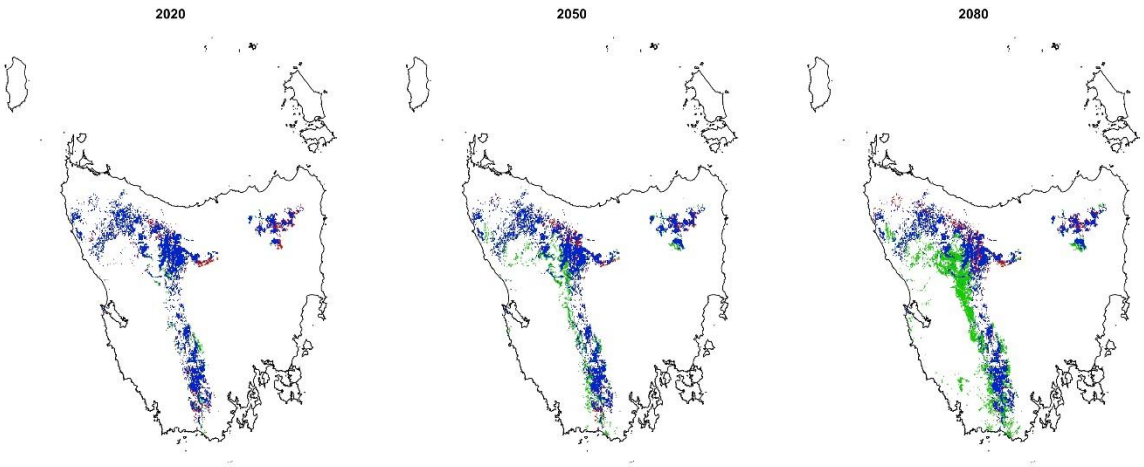
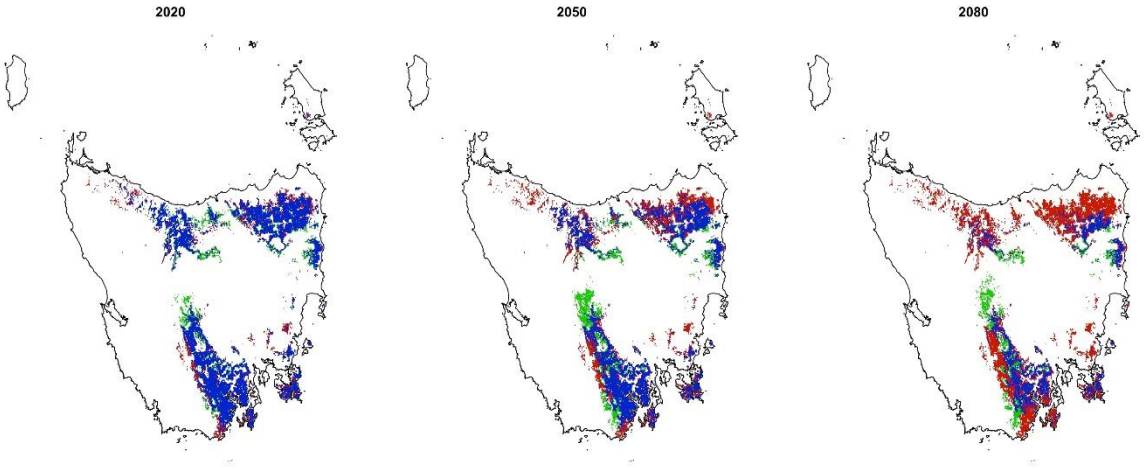
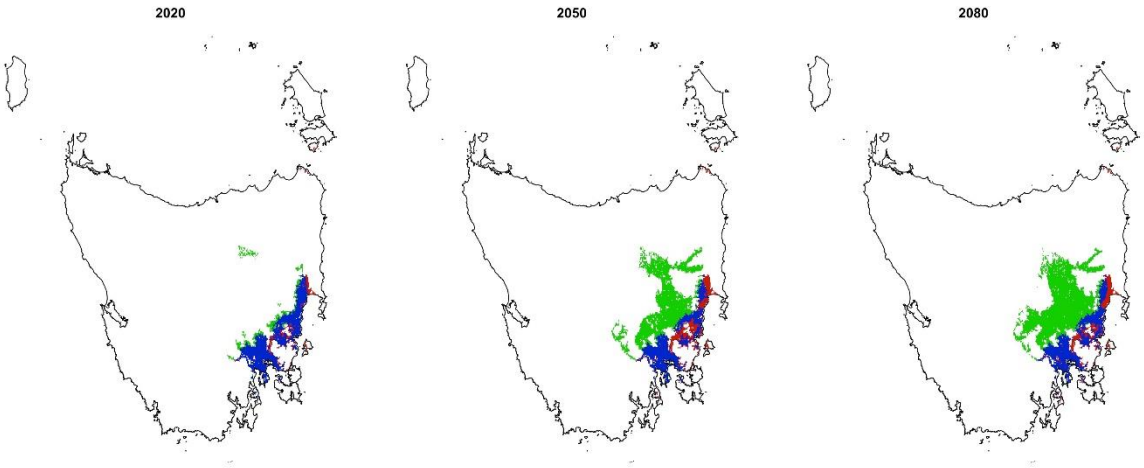


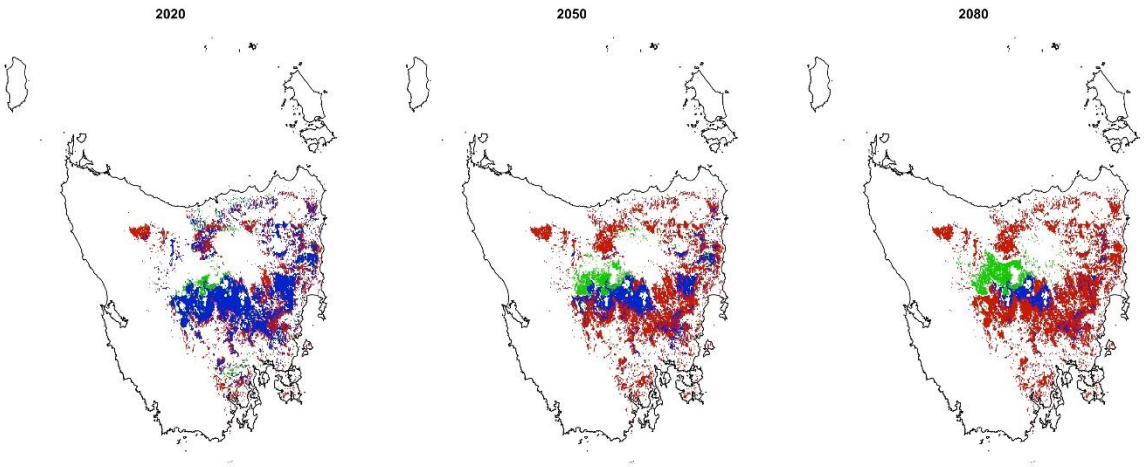
Eucalyptus regnans



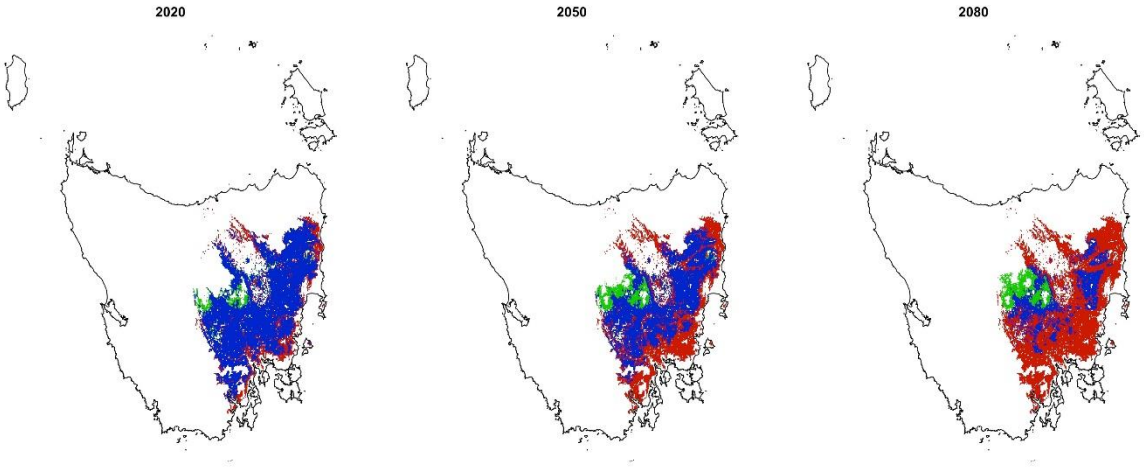
Eucalyptus risdonii



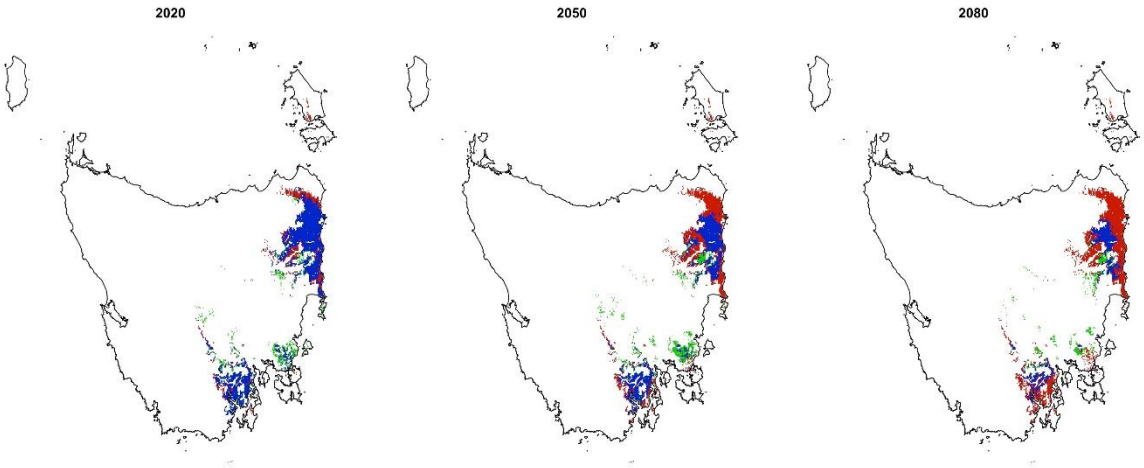
Eucalyptus rodwayi



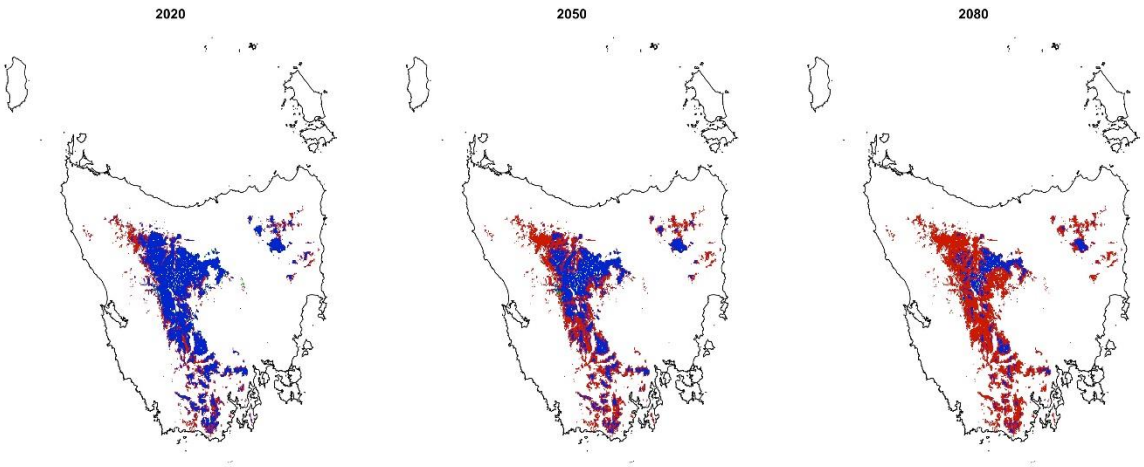
Eucalyptus rubida



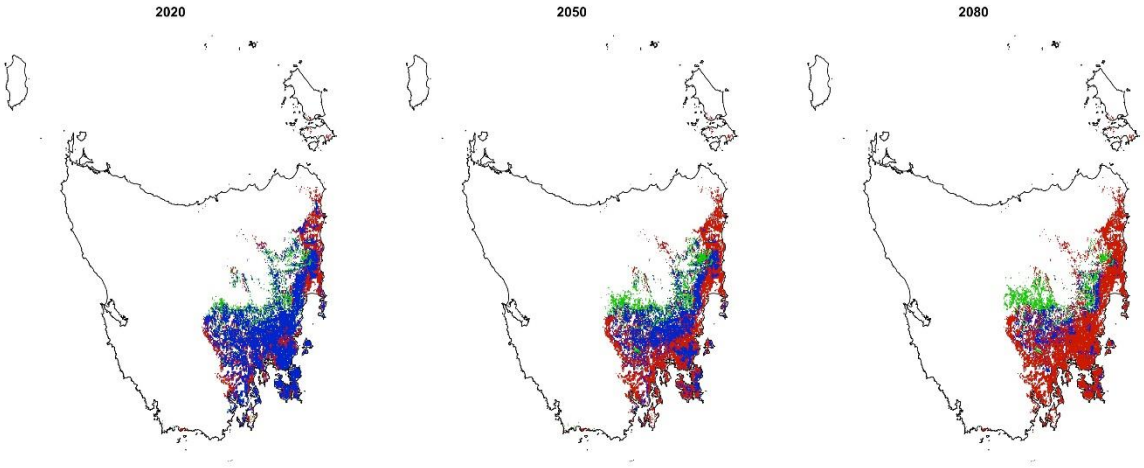
Eucalyptus sieberi



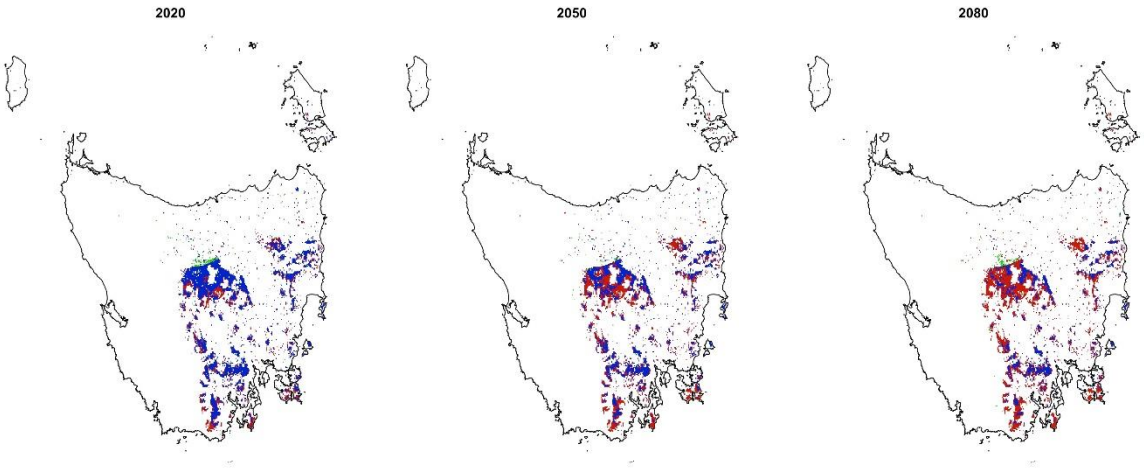
Eucalyptus subcrenulata



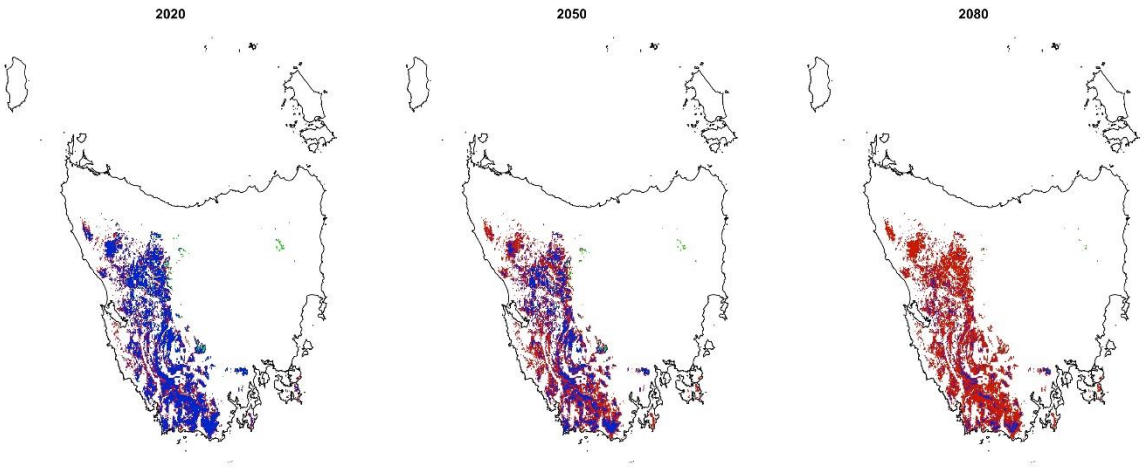
Eucalyptus tenuiramis



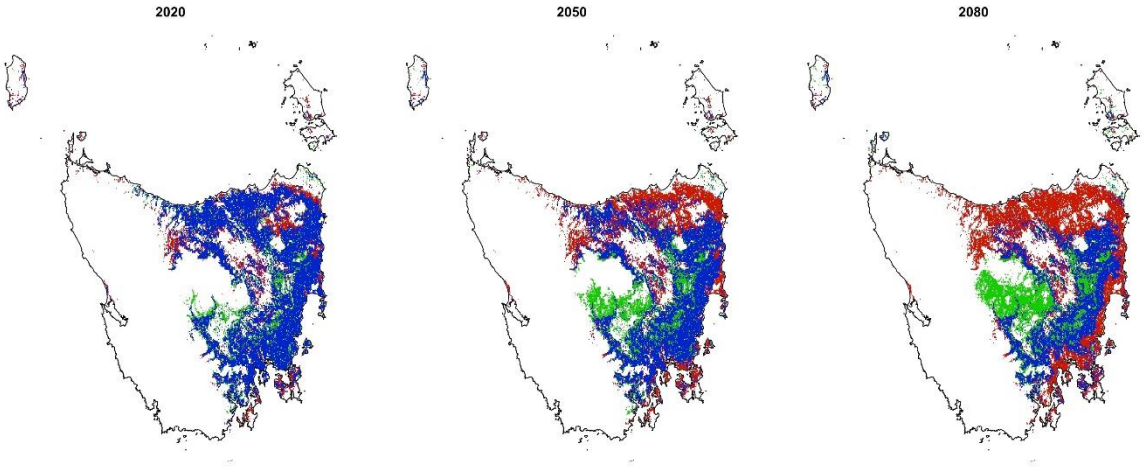
Eucalyptus unigera



Eucalyptus vernicosa

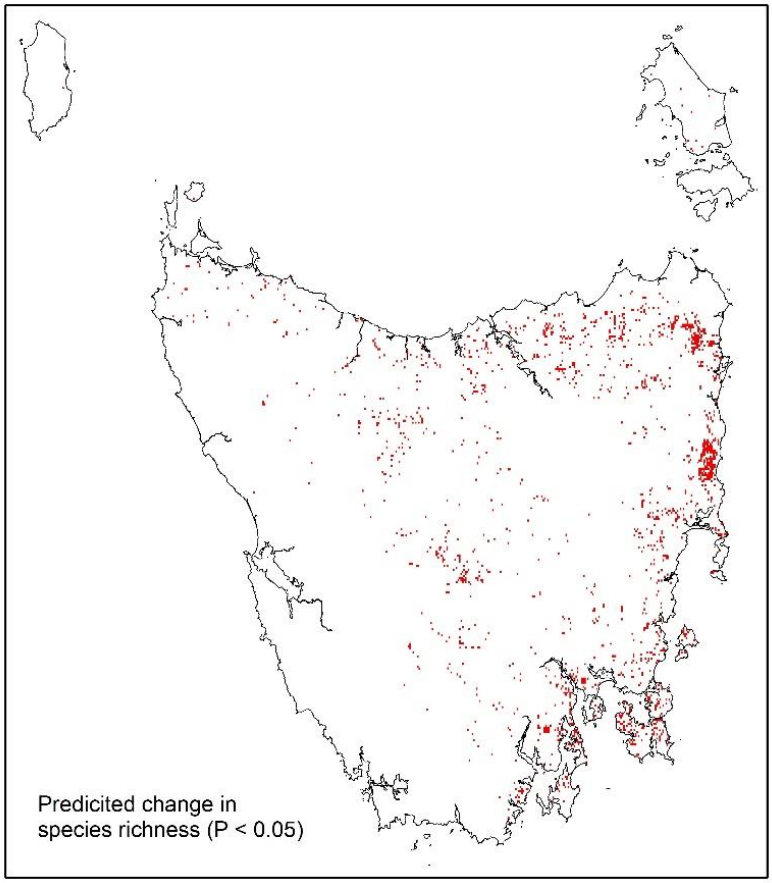


Eucalyptus viminalis



Supplementary material A6

The significant changes in species diversity between current (1976-2005) and future (2080s) predictions. Species diversity was calculated as the number of species within a 30 second grid cell that was within modelled suitable habitat.



Appendix B - Supplementary material for Chapter 3

Supplementary material B1

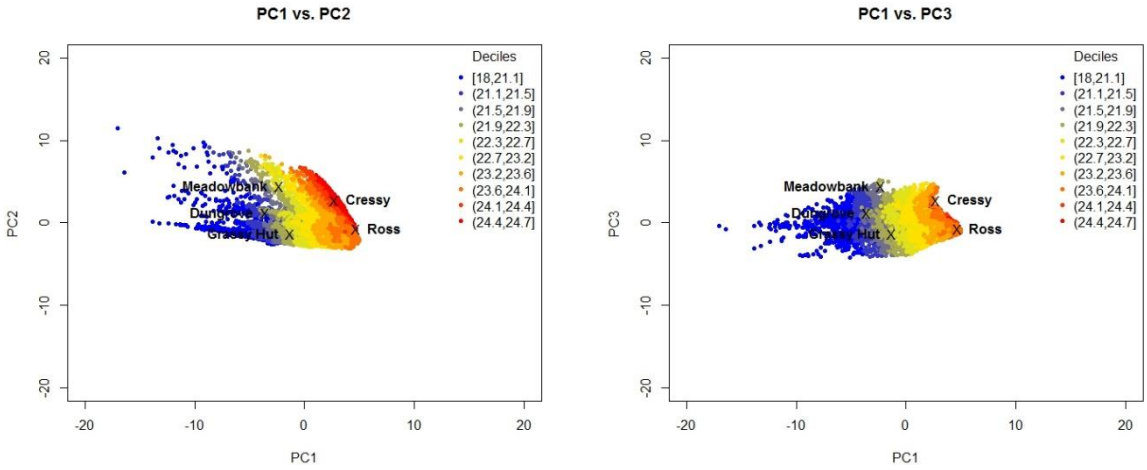
The 19 bioclimatic temperature and precipitation variables used to identify the underlying climate gradients across the Midlands region. The mean and range (in parenthesis) are given, along with the correlation coefficients of each bioclimatic variable against the first three principal components (PC) of the principal components analysis. Bold faced correlation coefficients represent the temperature and precipitation variable that had the highest absolute relationship with the PC and that was independent (i.e. $|r| < 0.5$) from other PC axes.

Variable	Code	Mean (range)	Variable correlations (loadings)		
			PC1	PC2	PC3
Mean annual temperature	TANN	10.7 (7.5 - 12.4)	0.80	0.13	0.58
Mean diurnal temperature range	TMDR	11.2 (8.6 - 12.4)	0.89	0.36	-0.21
Isothermality	TIT	0.5 (0.5 - 0.5)	0.87	-0.07	0.08
Temperature seasonality*	TCVAR	1.3 (1.1 - 1.3)	0.78	0.51	-0.28
Max temperature of warmest week	TMXWW	22.7 (18 - 24.7)	0.92	0.33	0.12
Min temperature of coldest week	TMNCW	1 (-0.5 - 2.8)	0.03	-0.30	0.94
Temperature annual range	TSPAN	21.7 (17.7 - 23.8)	0.85	0.42	-0.25
Mean temperature of wettest quarter	TWETQ	9.8 (3.9 - 15.1)	-0.06	-0.82	0.26
Mean temperature of driest quarter	TDRYQ	12.1 (4.6 - 16.2)	0.31	0.64	0.12
Mean temperature of warmest quarter	TWMQ	15.3 (11.6 - 16.8)	0.87	0.25	0.42
Mean temperature of coldest quarter	TCLQ	6.2 (3.5 - 8)	0.64	-0.02	0.76
Annual precipitation	RANN	585.1 (443.5 - 1168.4)	-0.74	0.64	0.17
Precipitation of wettest week	RWETW	14.4 (9.9 - 34.9)	-0.49	0.84	0.16
Precipitation of driest week	RDRYW	7.4 (5.5 - 12.9)	-0.93	0.08	0.16
Precipitation seasonality*	RCVAR	16.2 (11.1 - 29)	0.17	0.88	0.02
Precipitation of wettest quarter	RWETQ	173.2 (124.4 - 379.1)	-0.57	0.80	0.12
Precipitation of driest quarter	RDRYQ	120.5 (96.7 - 207.5)	-0.92	0.18	0.19
Precipitation of warmest quarter	RWMQ	132.7 (104.3 - 224.5)	-0.93	0.03	0.26
Precipitation of coldest quarter	RCLW	156.5 (109.4 - 370.7)	-0.49	0.84	0.17

* Coefficient of variation

Supplementary material B2

Summary of the climate variation in the Midlands of Tasmania. The first three principal components accounted for a cumulative total variance of 91%. Shown is the location of the five main ecological restoration projects that have been established over the past 10 years. Points represent the climate space of the Midlands and has been coloured based on the decile of maximum summer temperatures (TMXWW, Appendix B1).



Supplementary material B3

The climate variation across the Midlands was summarised by the first three axes of the PCA explained a cumulative total variance of 91%. The first axis (PC1) explained 51% of this variance and was related with the maximum temperature of the warmest week (TMXWW, loading = 0.92) and precipitation of the driest week (RDRYW, loading = -0.93) (Appendix B1). As peak precipitation in the Midlands tends to occur during the winter months, the opposing combination of TMXWW and RDRYW suggested PC1 represented a summer aridity gradient across the Midlands. Similarly, mean temperature of the wettest quarter (TWETQ, loading = -0.82) and precipitation of the coldest quarter (RCLQ, loading = 0.84) were strongly correlated with PC2, which explained 27% of the variance in the second dimension (Appendix B1). The opposing combination of TWETQ and RCLQ suggested PC2 represented a winter aridity gradient across the Midlands, which was orthogonal to the summer aridity gradient. The third axis (PC3) was only strongly correlated with winter-associated temperature variables and explained 13% of the variance, with its greatest correlation occurring with minimum temperature of the coldest week (TMNCW, loading = 0.94) (Appendix B1). This suggested that values on PC3 represented a gradient of decreasing frost occurrence across the Midlands.

Supplementary material B4

Under the high emission scenario, the climate space of the Midlands is predicted to move on average 2.7 units along PC1 and 6.8 units along PC3 by the end of the century (Figure 3.4). The positive shift of the Midlands climate space corresponded with a projected 2.4°C increase in TMXWW, 0.2mm increase in RDRYQ, and 2.3°C increase in TMNCW (Figure 3.4). Positive changes in the climate space of the Midlands suggest the regions will become increasingly arid during summer (mainly through increasing temperatures) with decreased frost occurrences under future climate change. However, little change was detected in the climate space of the Midlands along PC2. Although changes in PC2 were not spatial uniform with increasing winter aridity in the northern Midlands (Figure 3.4), the stability of the winter aridity gradient with time suggests the climate space of the Midlands under future climates will disproportionate shift in response to positive changes in summer aridity and decreasing frost occurrences.

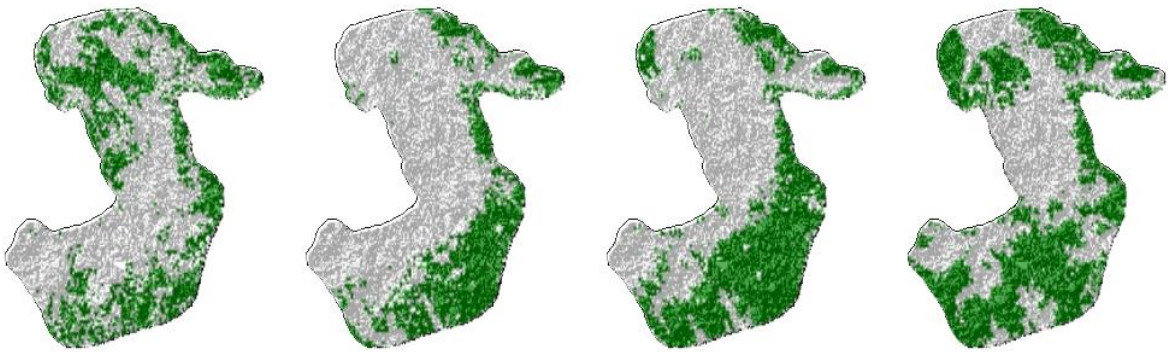
Supplementary material B5

The low error rate (mean squared error = 0.07) and high discrimination ability (Gini = 0.99) of the Random Forest model suggests it was able to accurately predict the distribution of the Midlands climate envelope. The model was able to account for 72% of the climate variance across the Midlands, with minimum cold temperature and winter precipitation being the most important variables in the model (data not shown). As expected, the spatial prediction of the model under current climate conditions showed a tight geographic clustering of high probability of suitable climate in the Midlands geographic region, with high probability of similar climate on the east side of the Eastern Tiers (data not shown). There was a progressive shift in the probability of the Midlands climate envelope through time, with the northern and southern Midlands predicted to be outside the current Midlands climate (i.e. decreasing probability values; Figure 3.5). By the end of this century, the climate envelope of the Midlands is predicted to redistribute up the Derwent Valley and onto the Central Plateau (Figure 3.5). As the Midlands is currently the most arid region in Tasmania, the regional model and PCA together suggest the trajectory of the Midlands may be one of increasingly aridity through time under future climates.

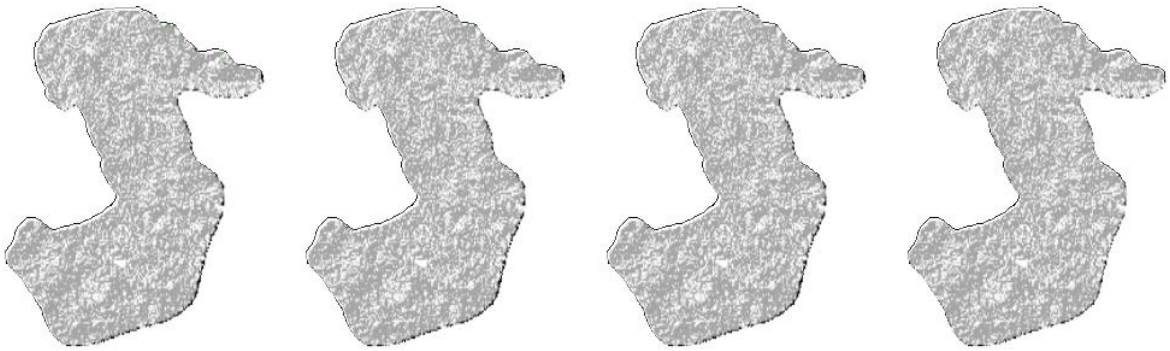
Supplementary material B6

Modelled suitable habitat within the Tasmanian Midlands for the 27 *Eucalyptus* species native to Tasmania. The green grid cells represent suitable habitat while the grey grid cells represent habitat that was not modelled as suitable.

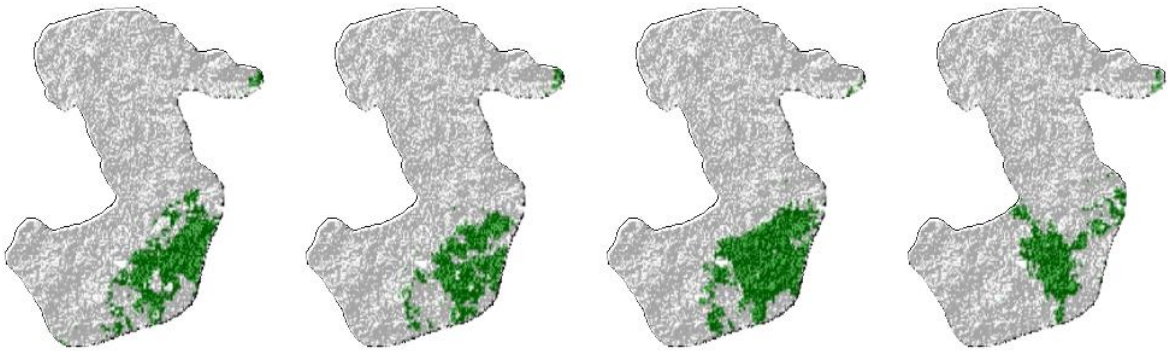
Eucalyptus amygdalina



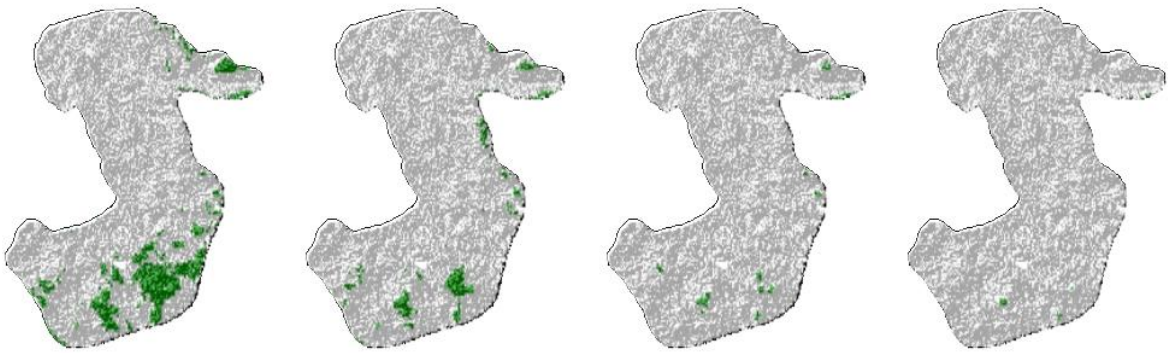
Eucalyptus archeri



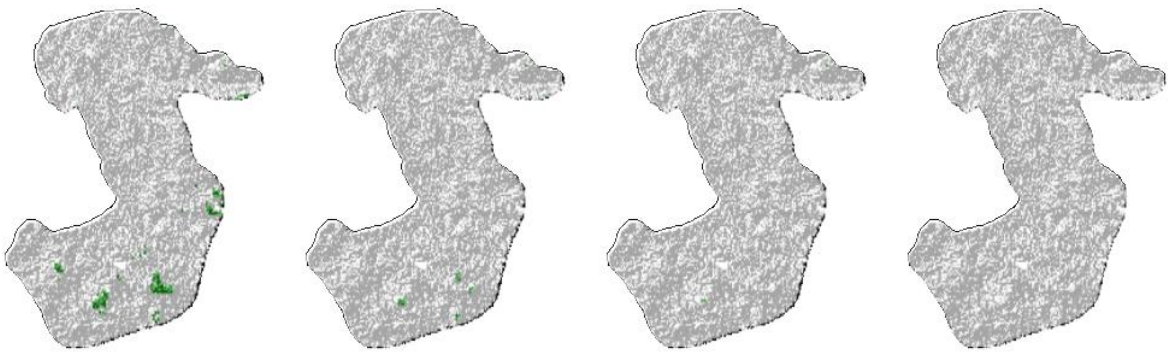
Eucalyptus barberi



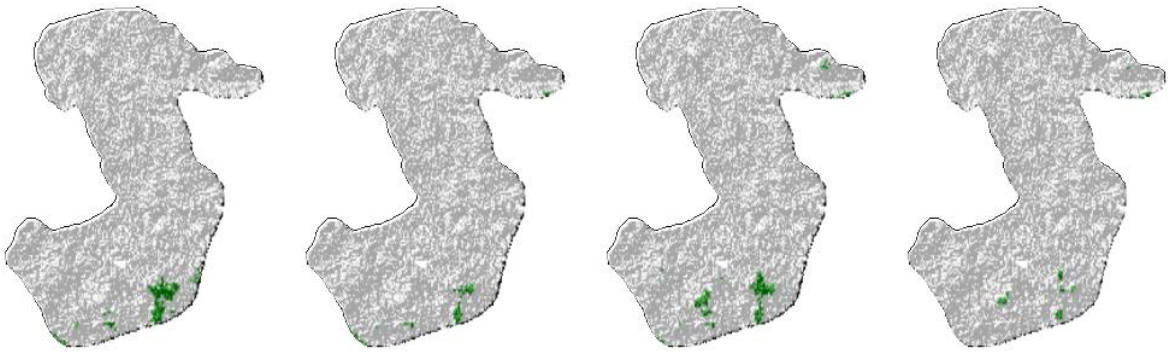
Eucalyptus brookeriana



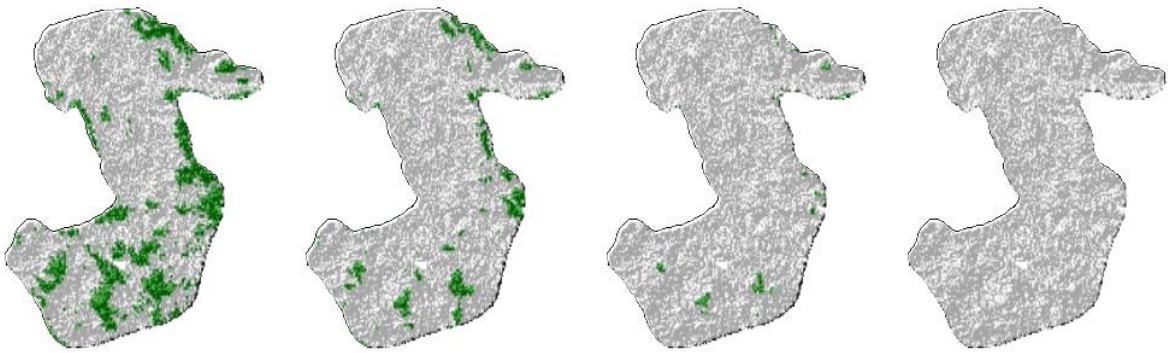
Eucalyptus coccifera



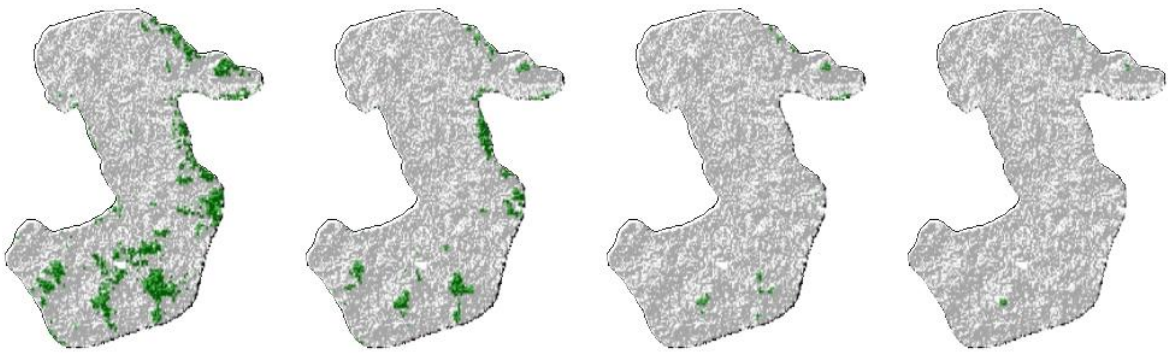
Eucalyptus cordata



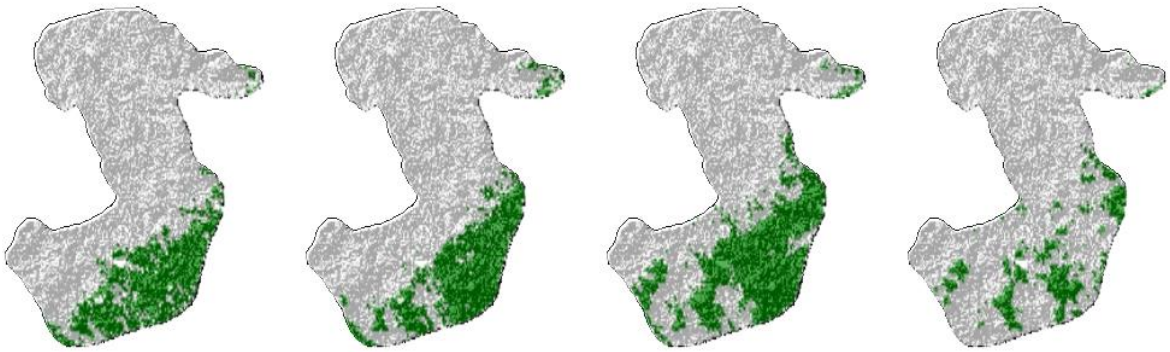
Eucalyptus dalrympleana



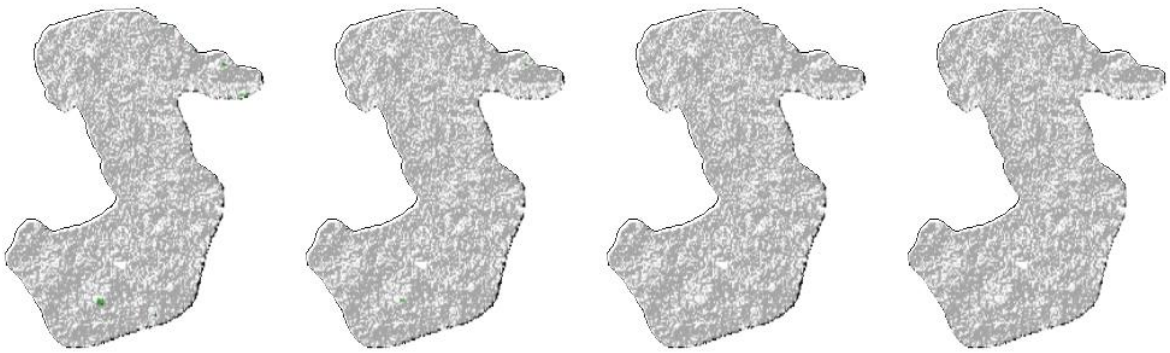
Eucalyptus delegatensis



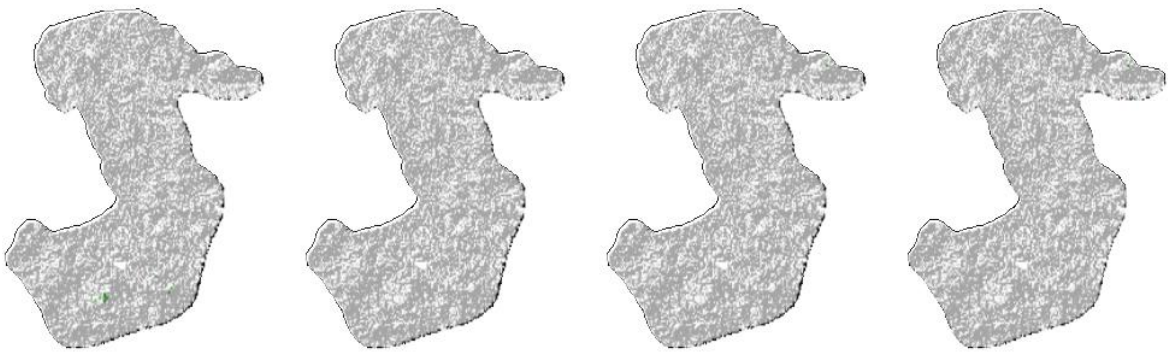
Eucalyptus globulus



Eucalyptus gunnii



Eucalyptus johnstonii



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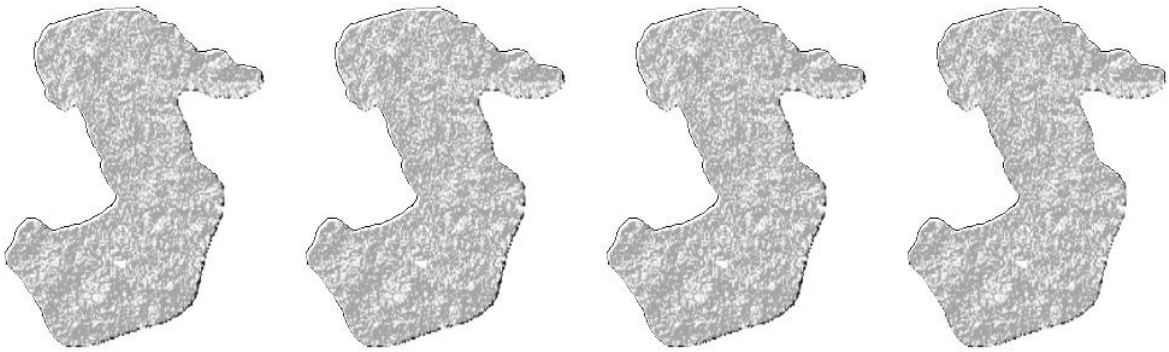

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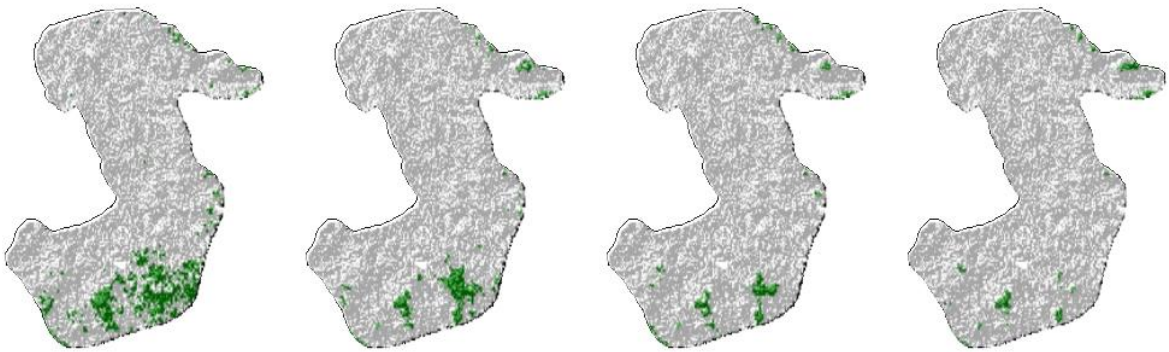
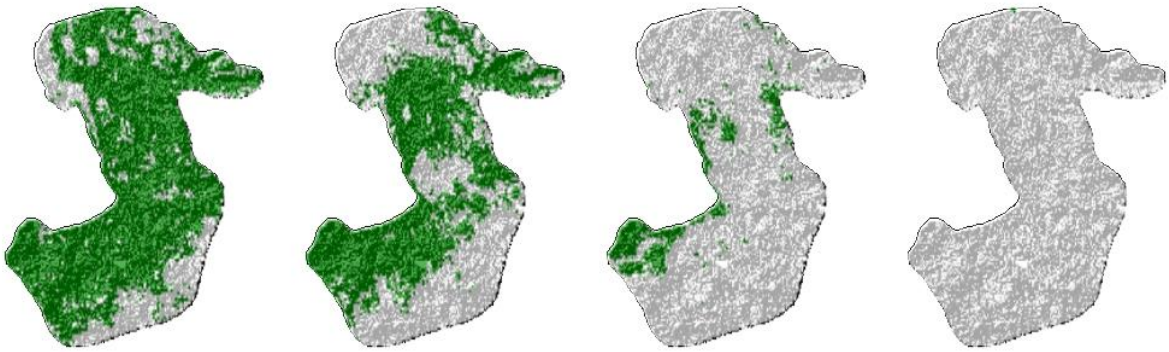
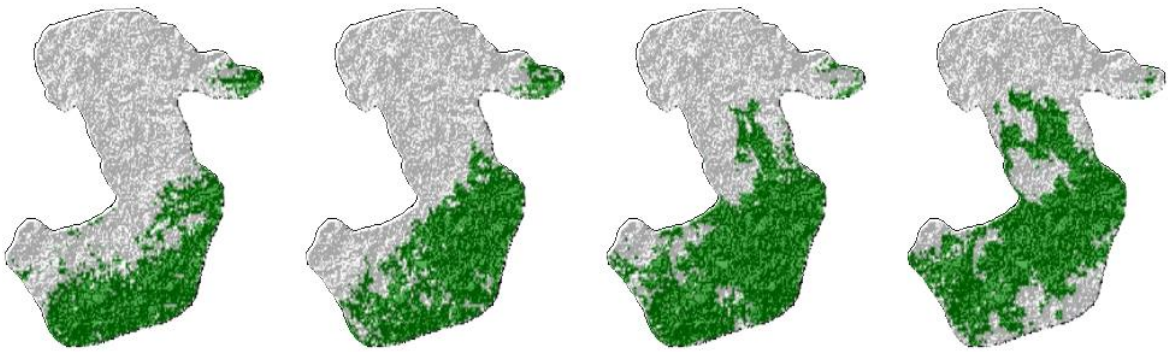


Eucalyptus ovata

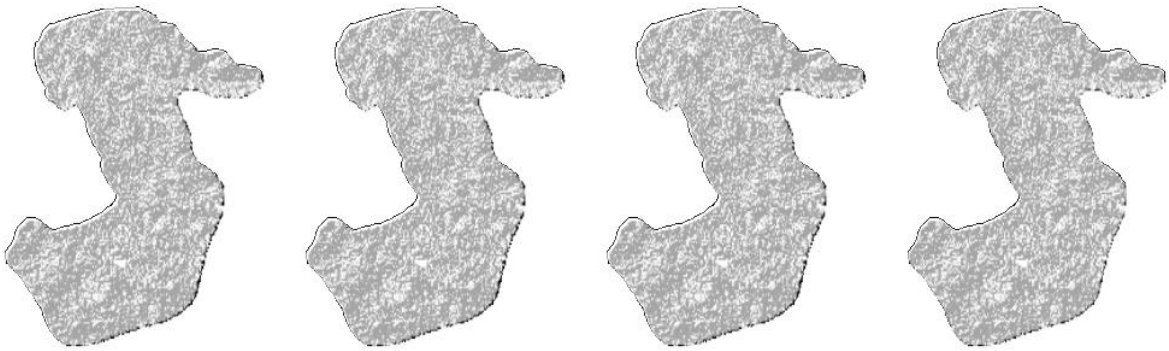
Eucalyptus pauciflora



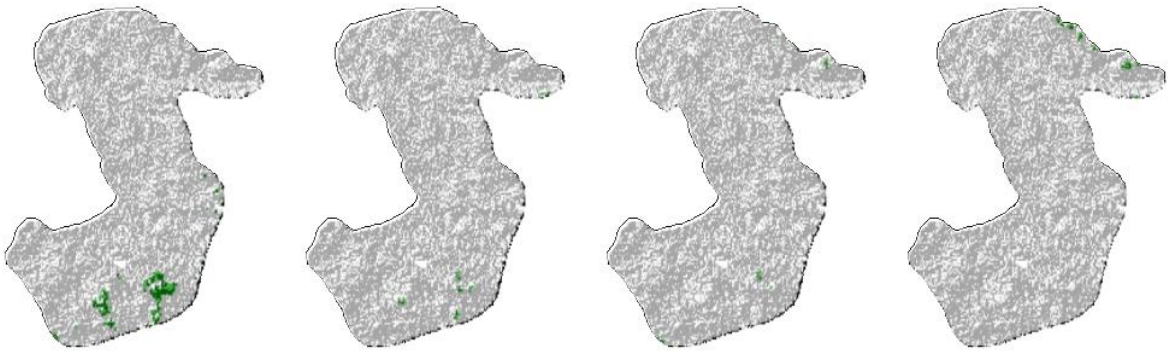
Eucalyptus pulchella



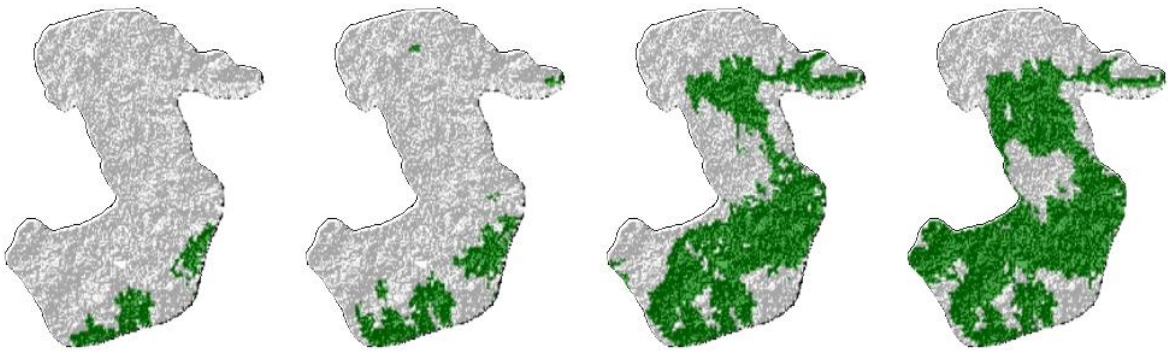
Eucalyptus radiata



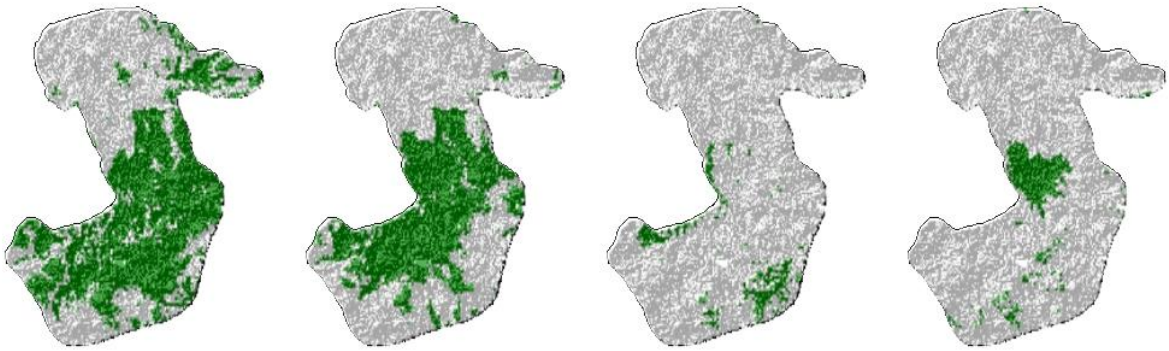
Eucalyptus regnans



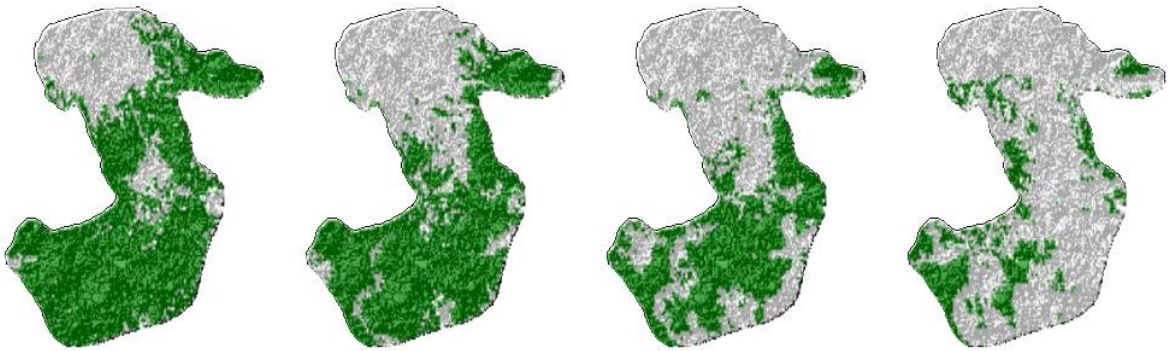
Eucalyptus risdonii



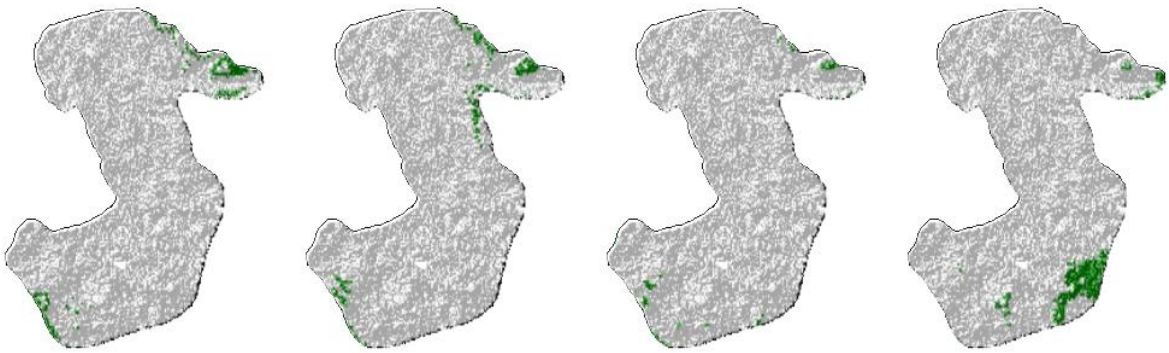
Eucalyptus rodwayi



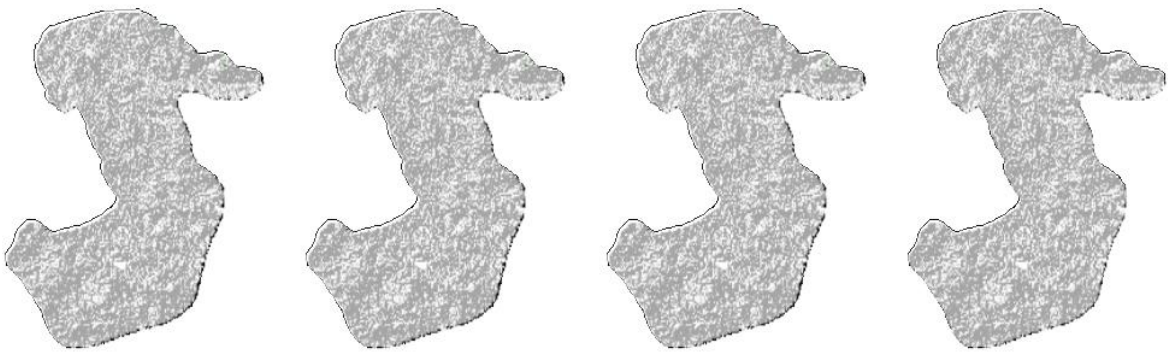
Eucalyptus rubida



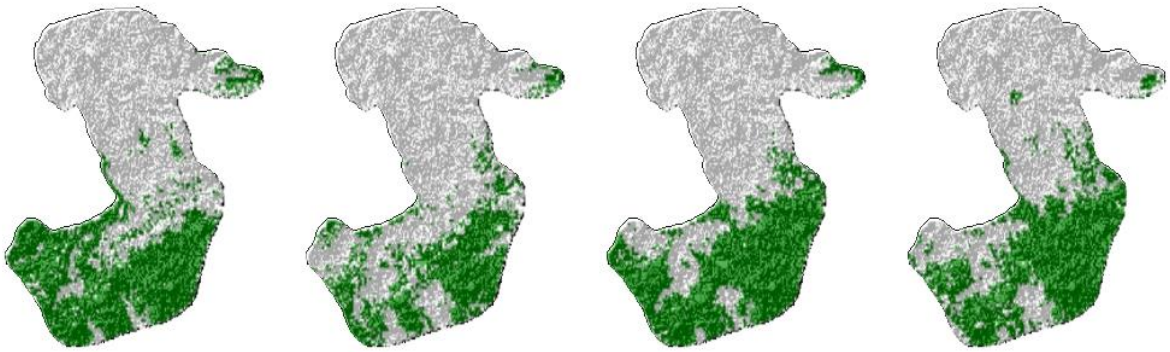
Eucalyptus sieberi



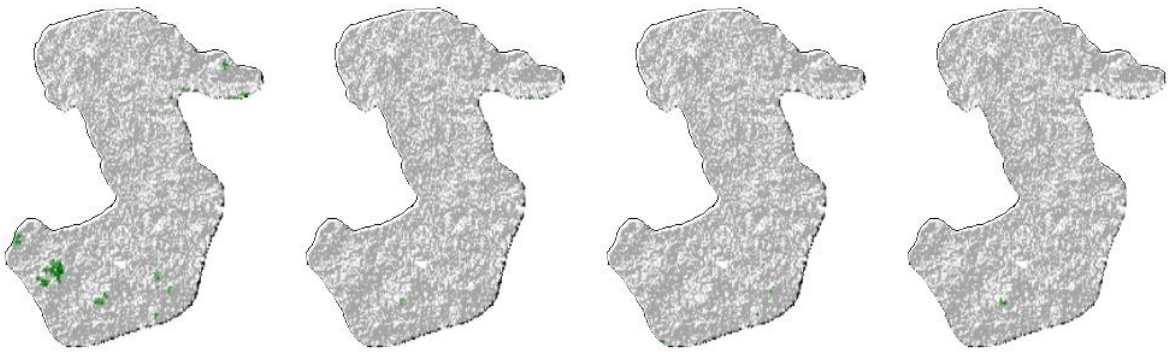
Eucalyptus subcrenulata



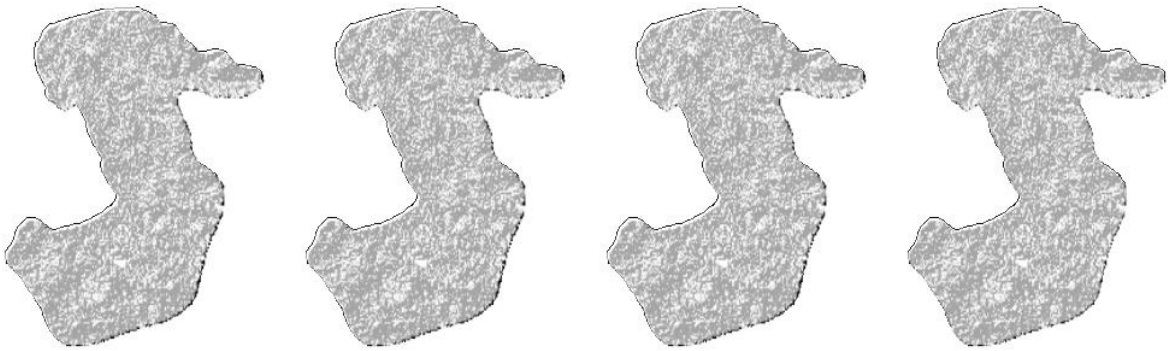
Eucalyptus tenuiramis



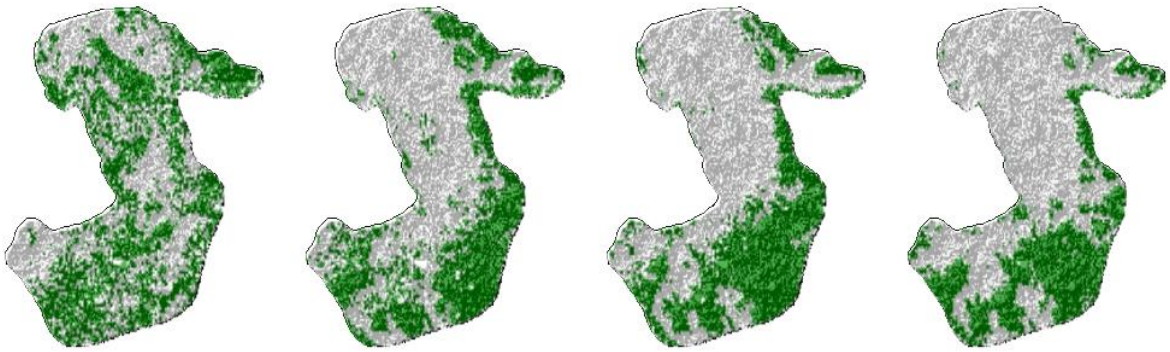
Eucalyptus urnigera



Eucalyptus vernicosa



Eucalyptus viminalis

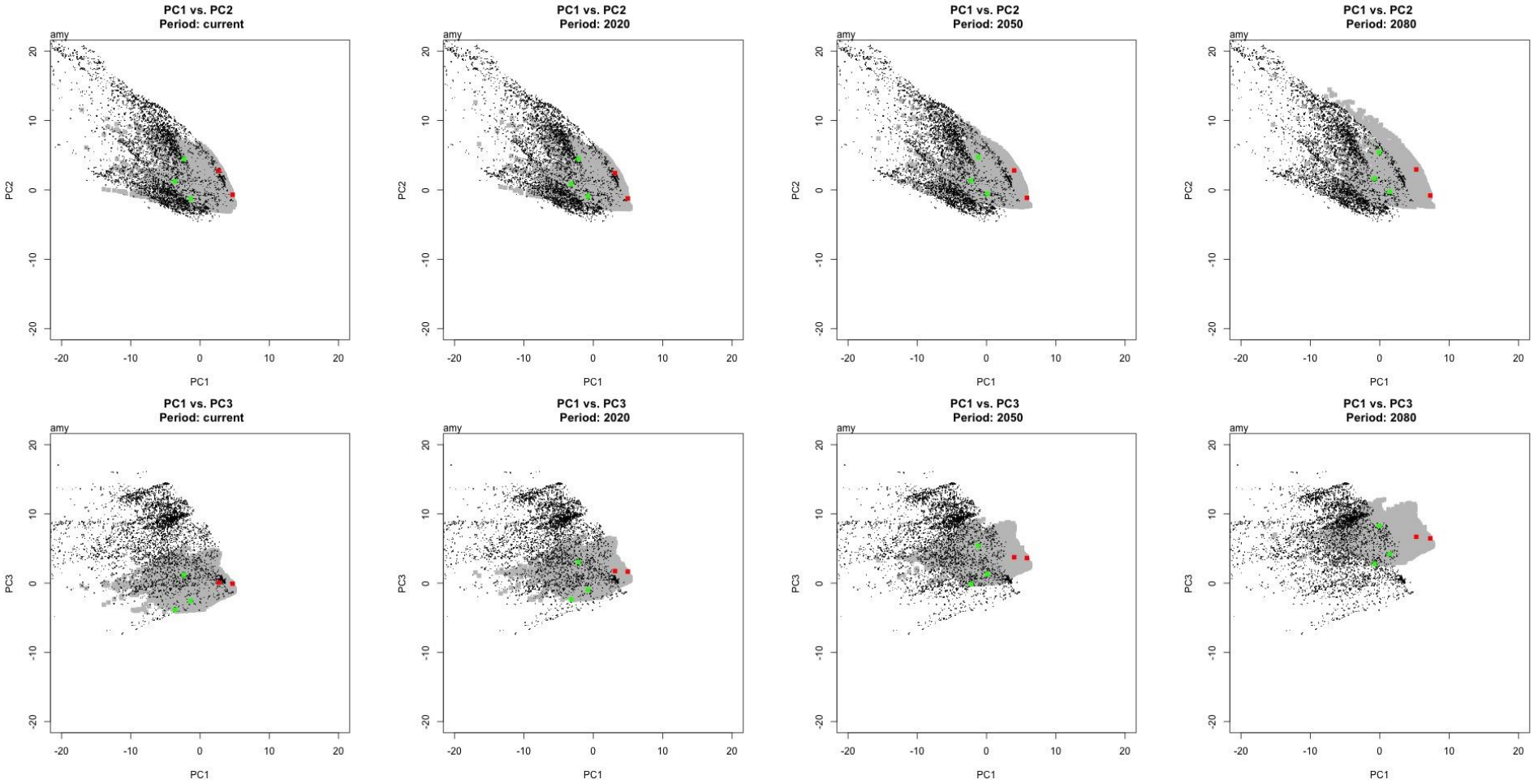


Supplementary material B7

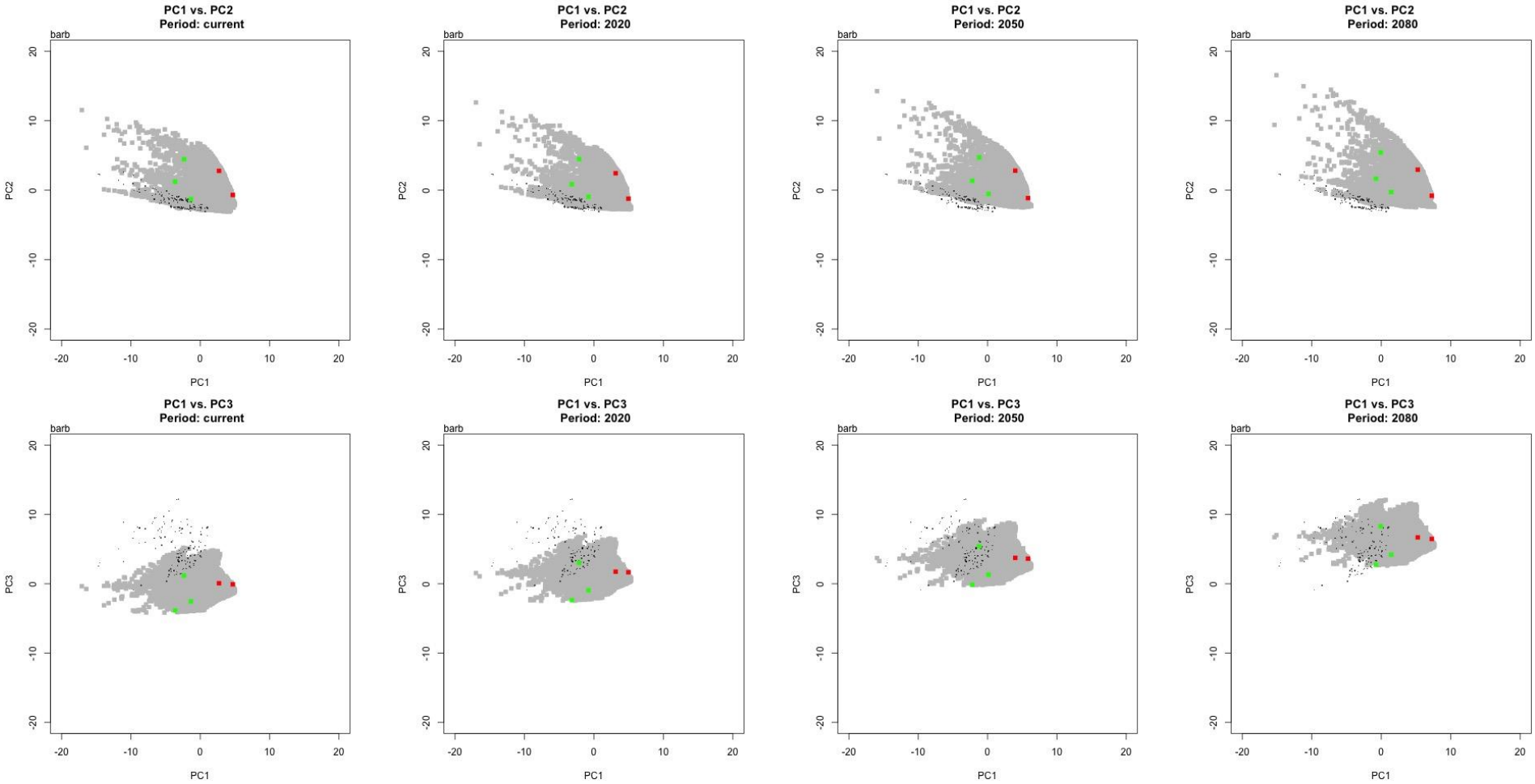
Change in the Midlands climate space through time. Shown are the two-dimensional plots of principal component (PC) 1 *versus* 2 and PC1 *versus* 3. The grey squares represent the climate space of the Tasmanian Midlands in the multidimensional PC space, and the black points represent the occurrence records for each of the 27 eucalypt species native to Tasmania. The red squares represent recent restoration sites in the northern Midlands, and the green squares represent recent restoration sites in the southern Midlands.

(Figures over page)

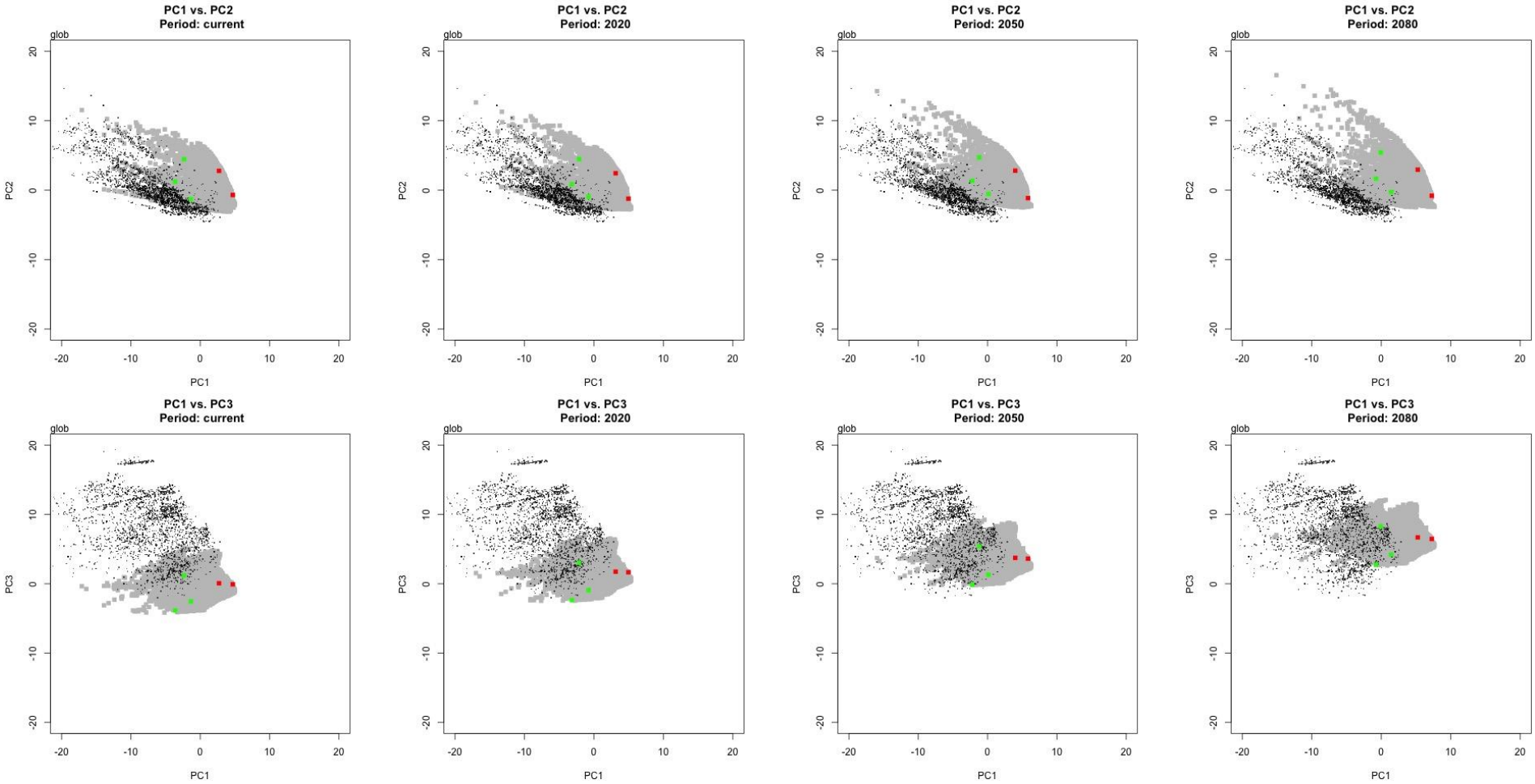
Eucalyptus amygdalina



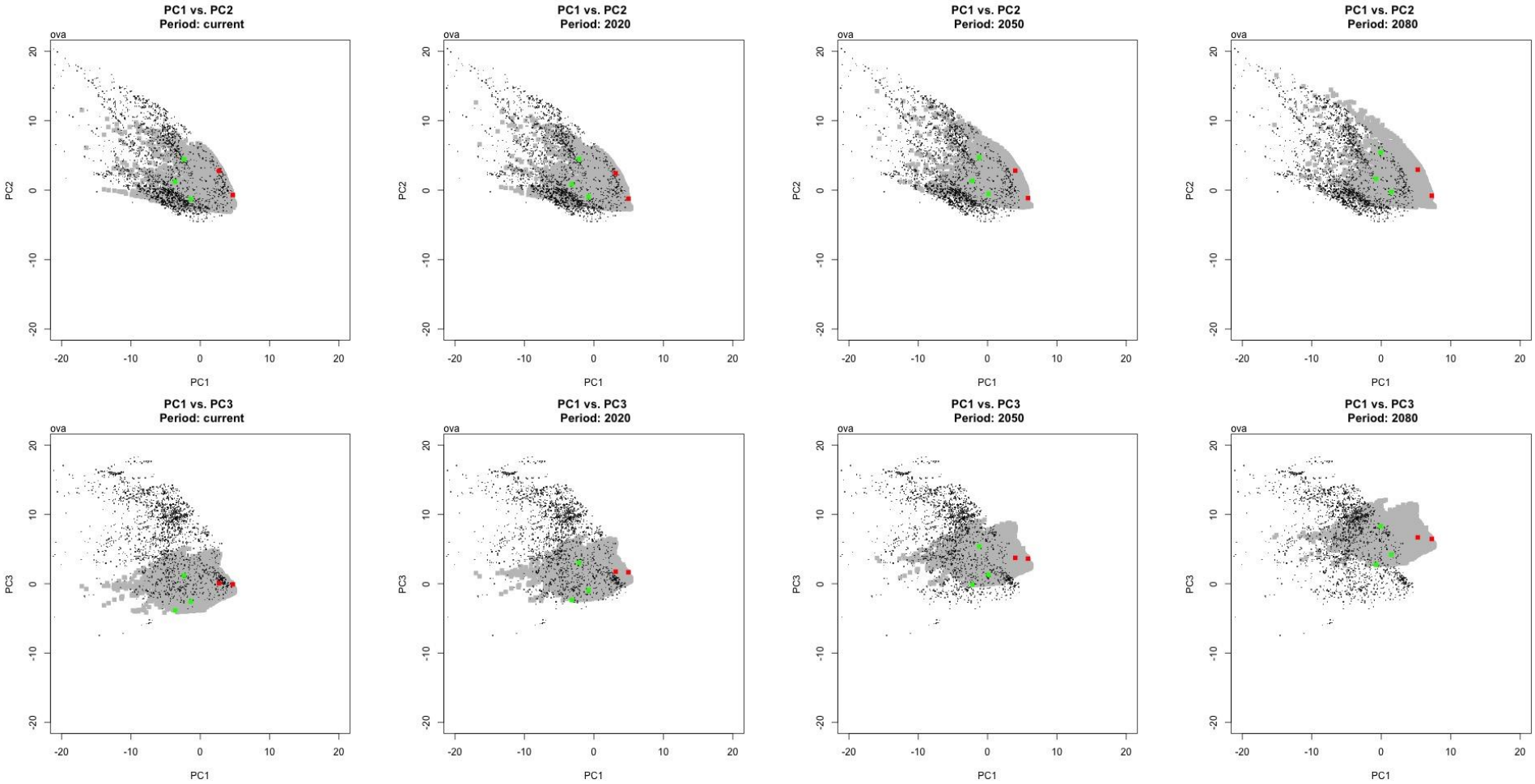
Eucalyptus barberi



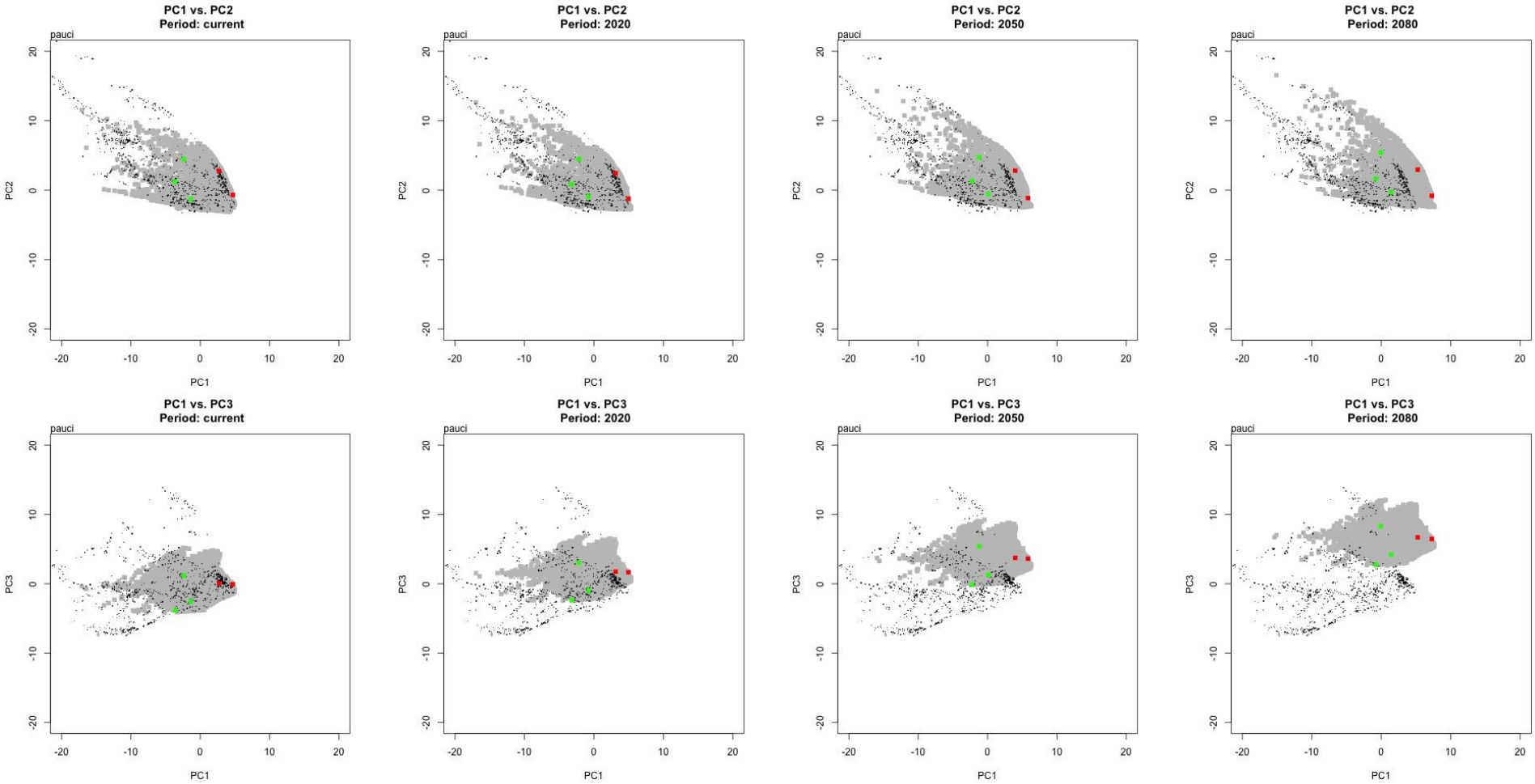
Eucalyptus globulus



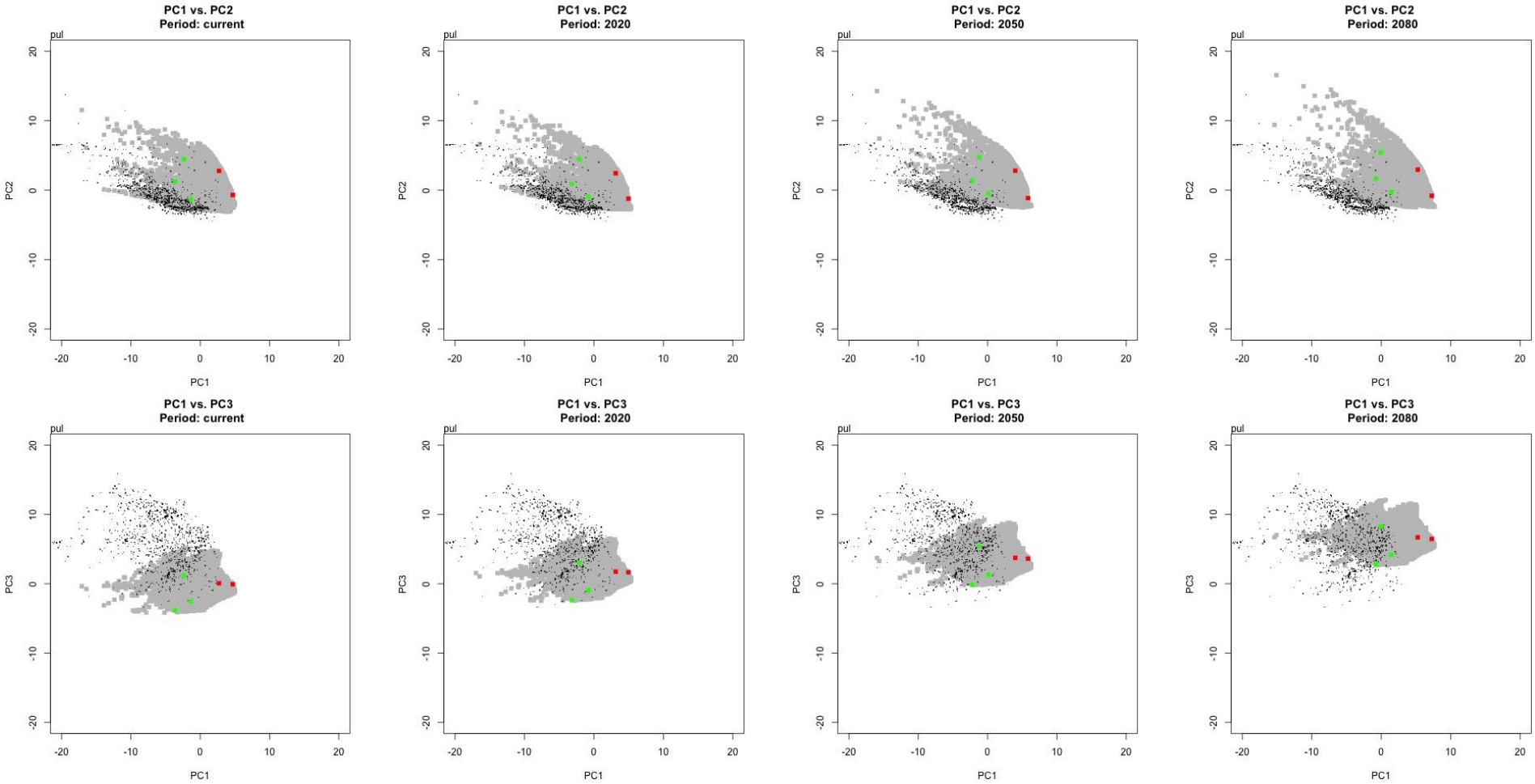
Eucalyptus ovata



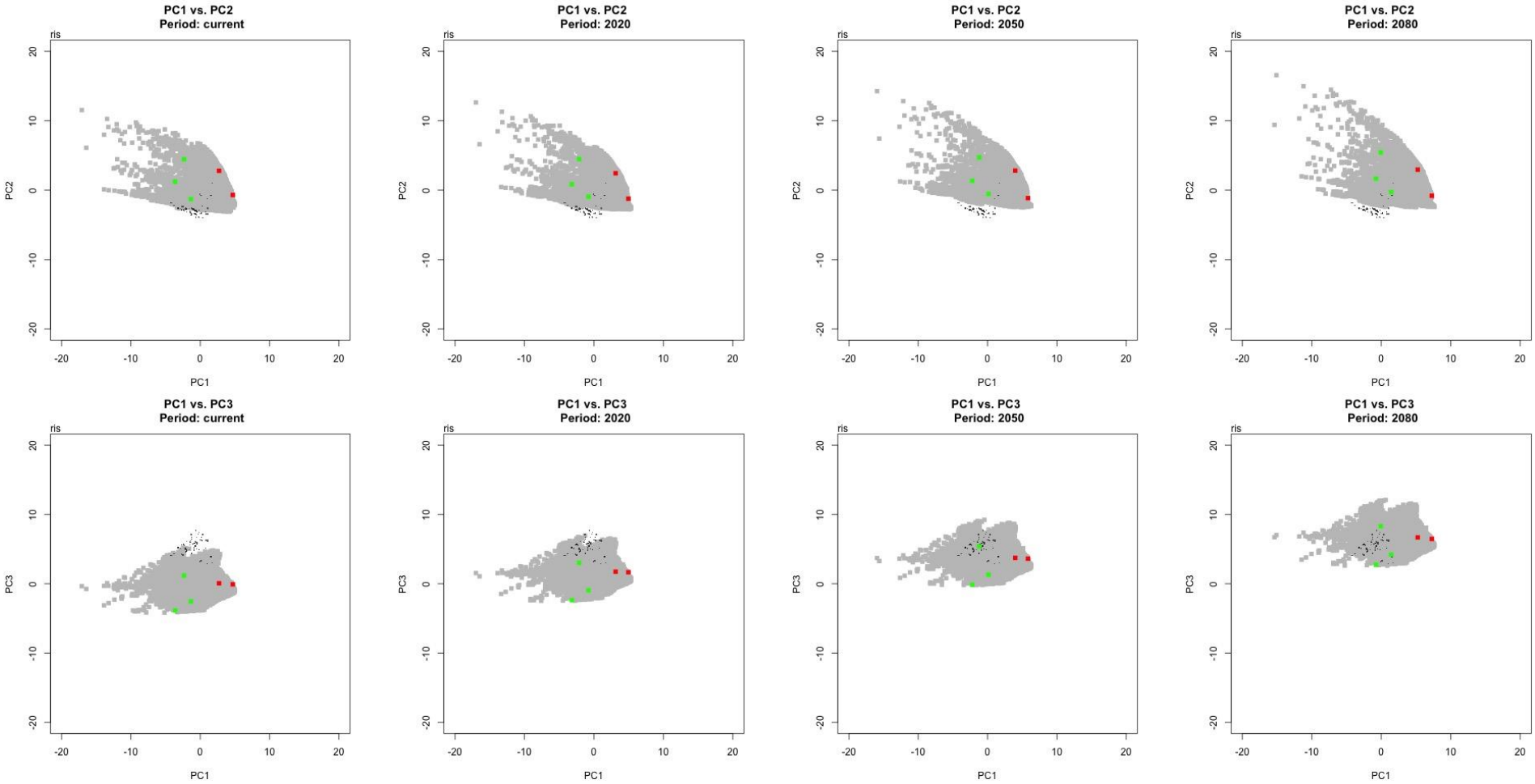
Eucalyptus pauciflora



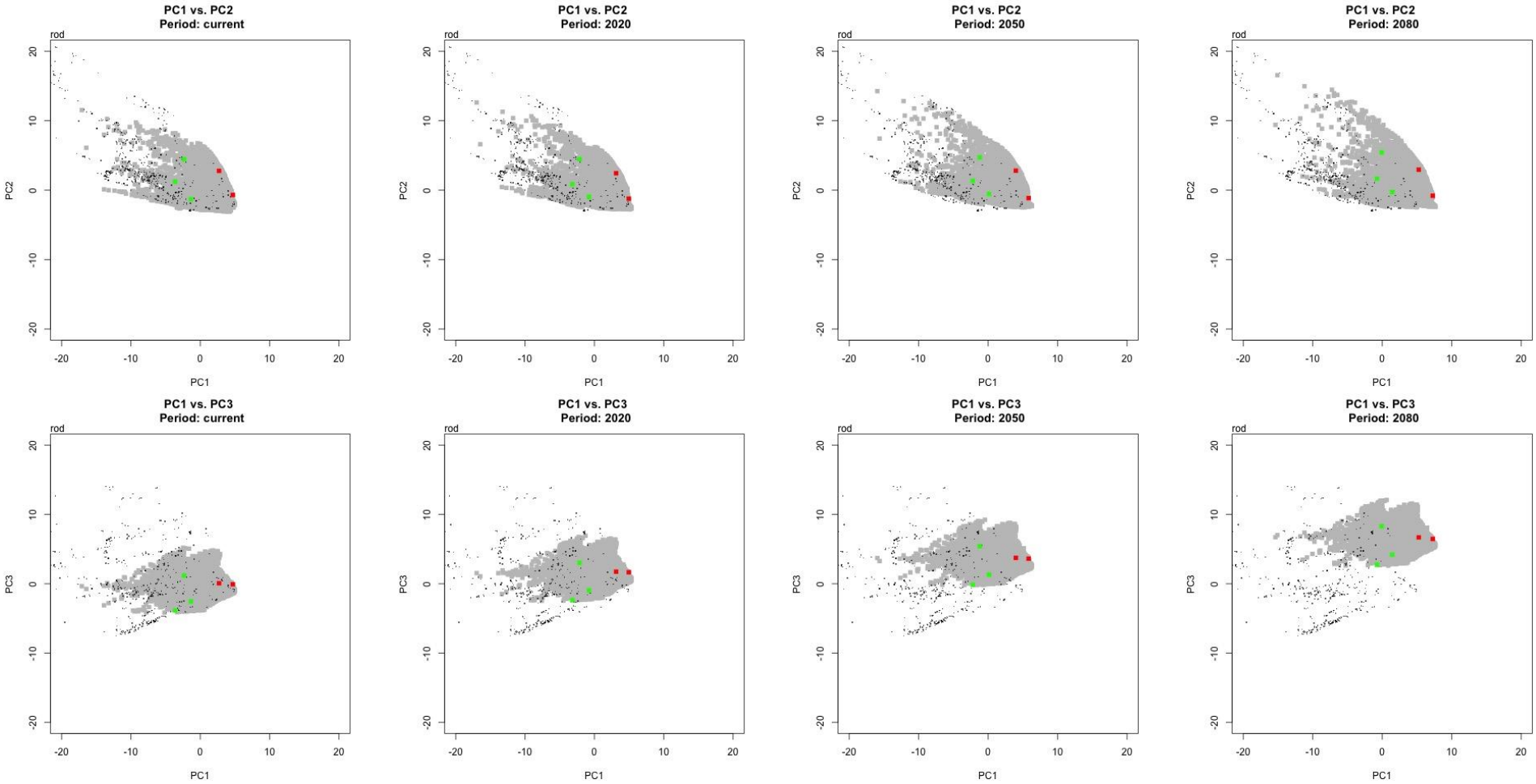
Eucalyptus pulchella



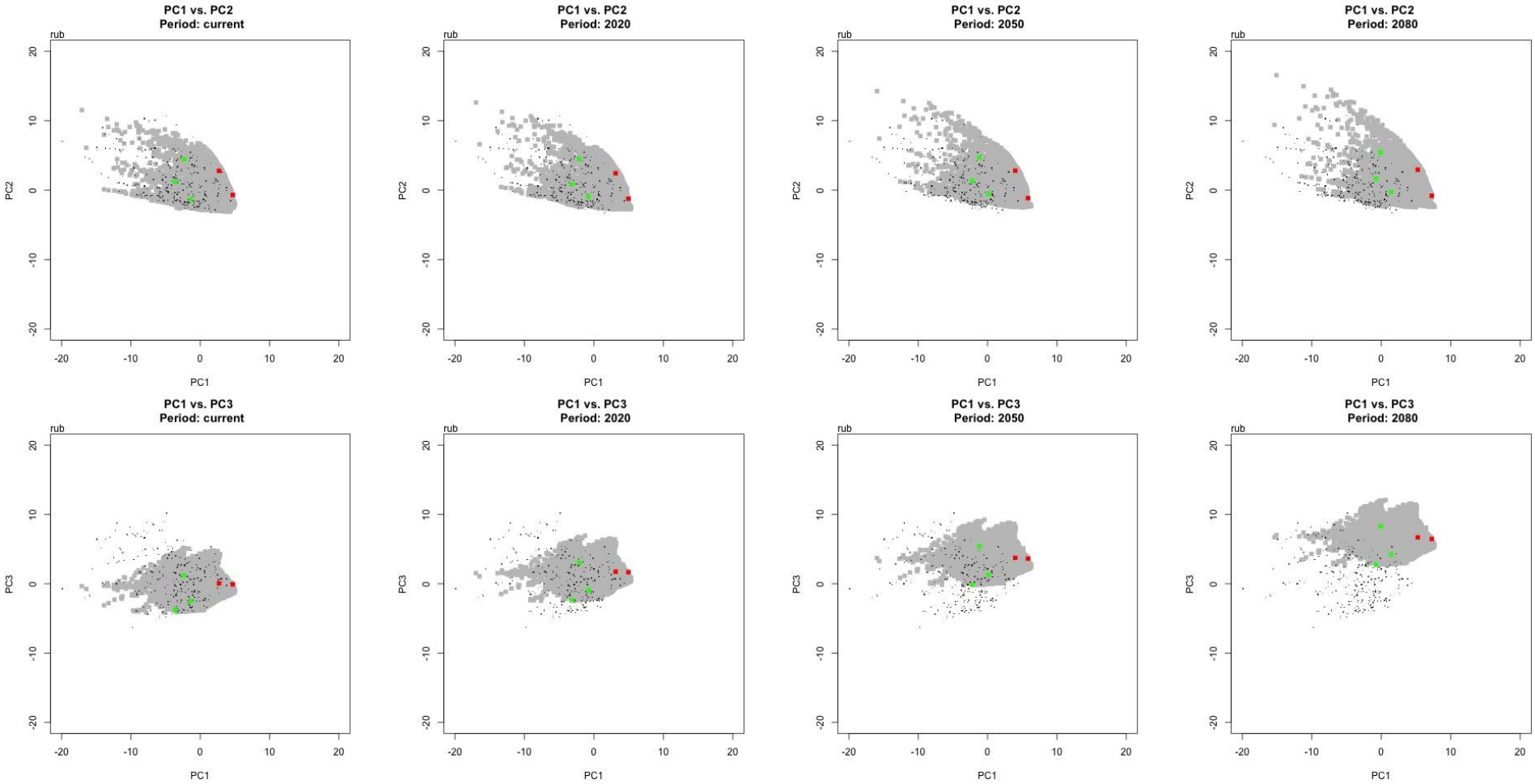
Eucalyptus risdonii



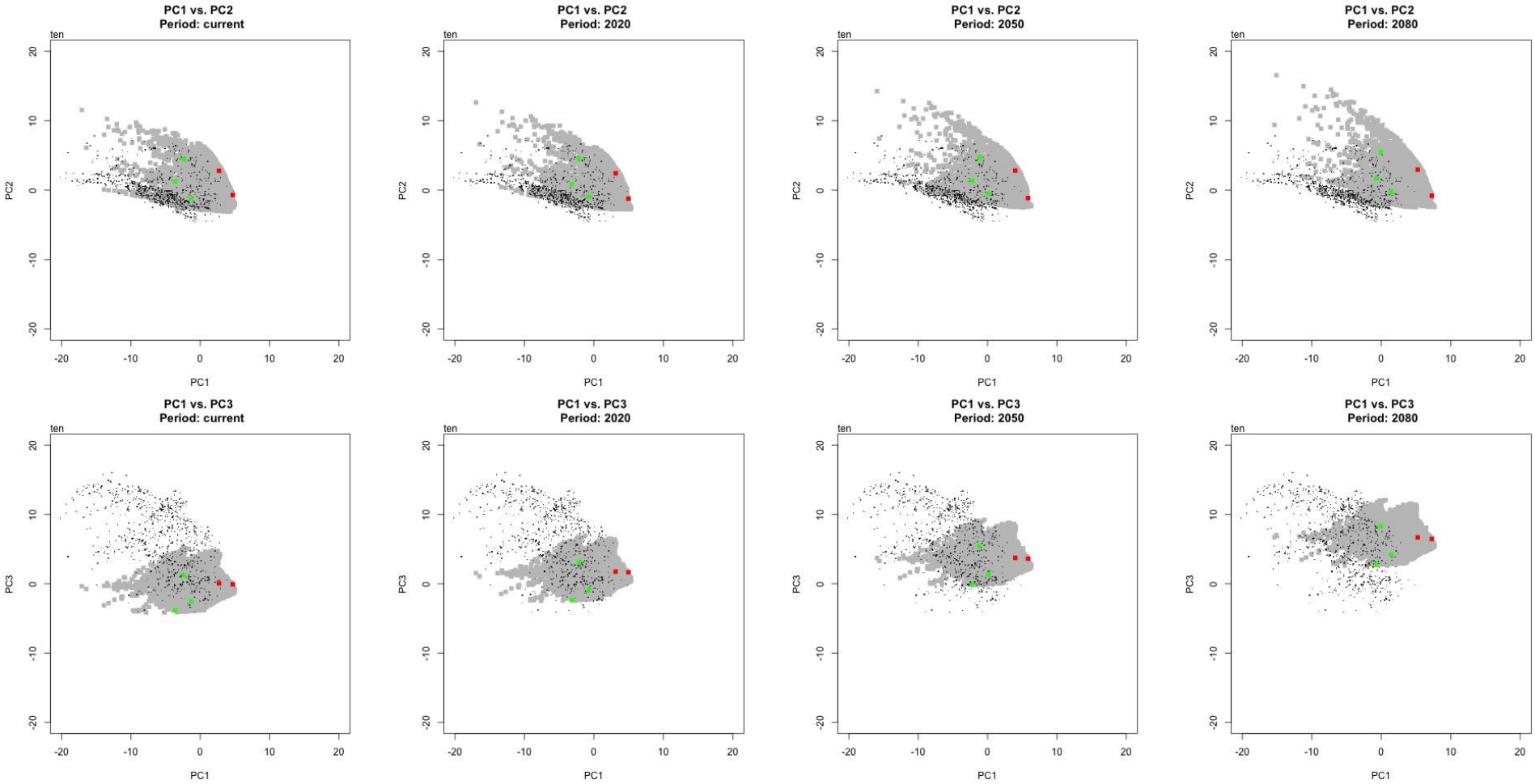
Eucalyptus rodwayi



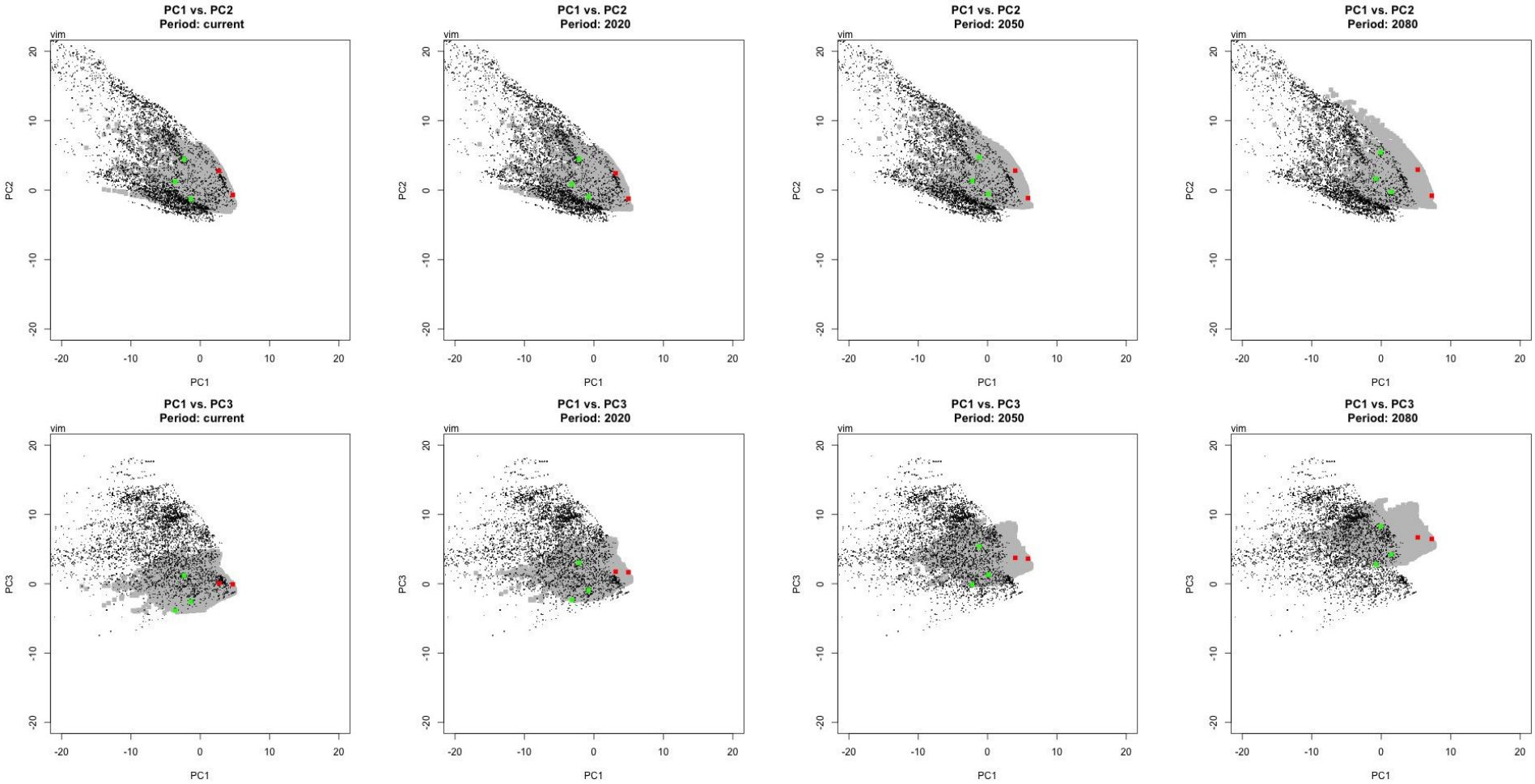
Eucalyptus rubida



Eucalyptus tenuiramis



Eucalyptus viminalis



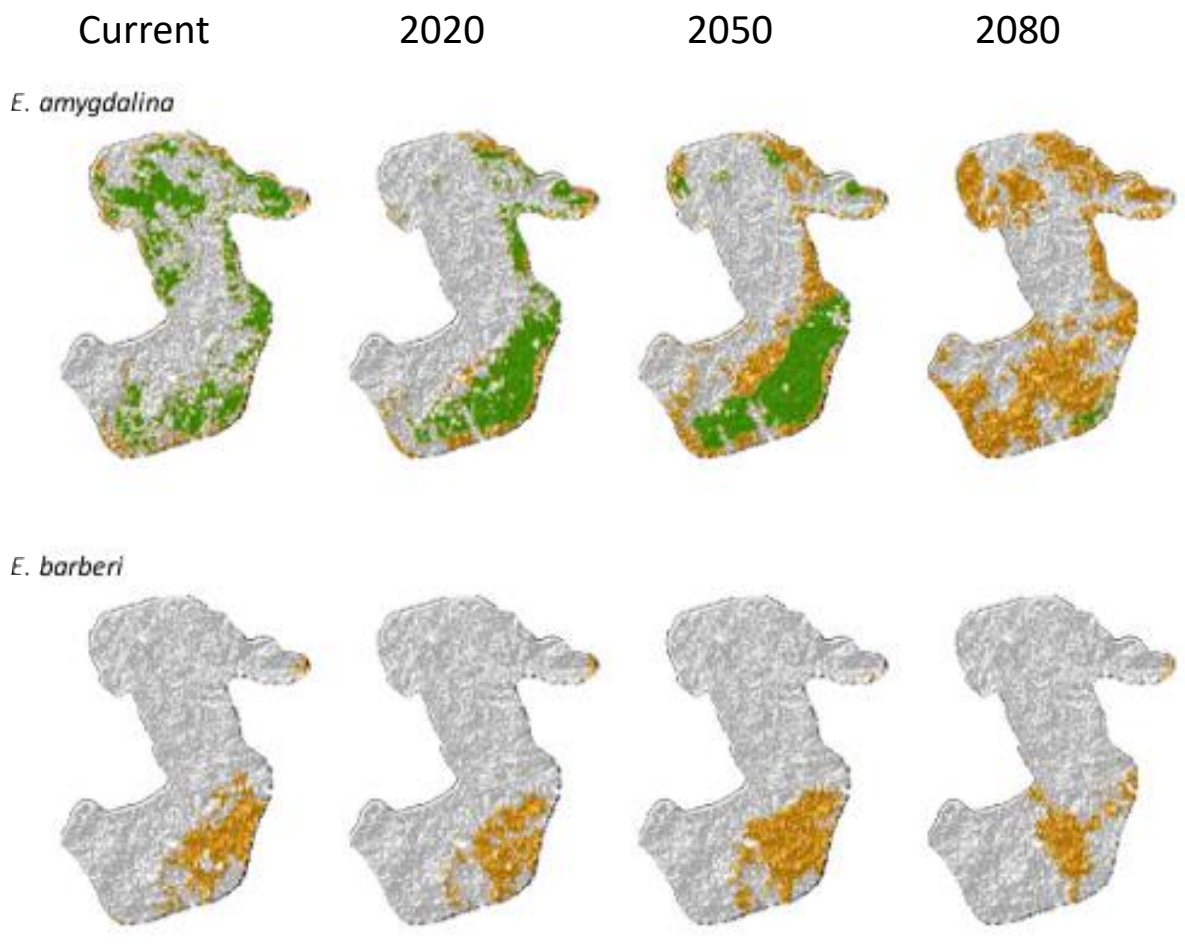
Supplementary material B8

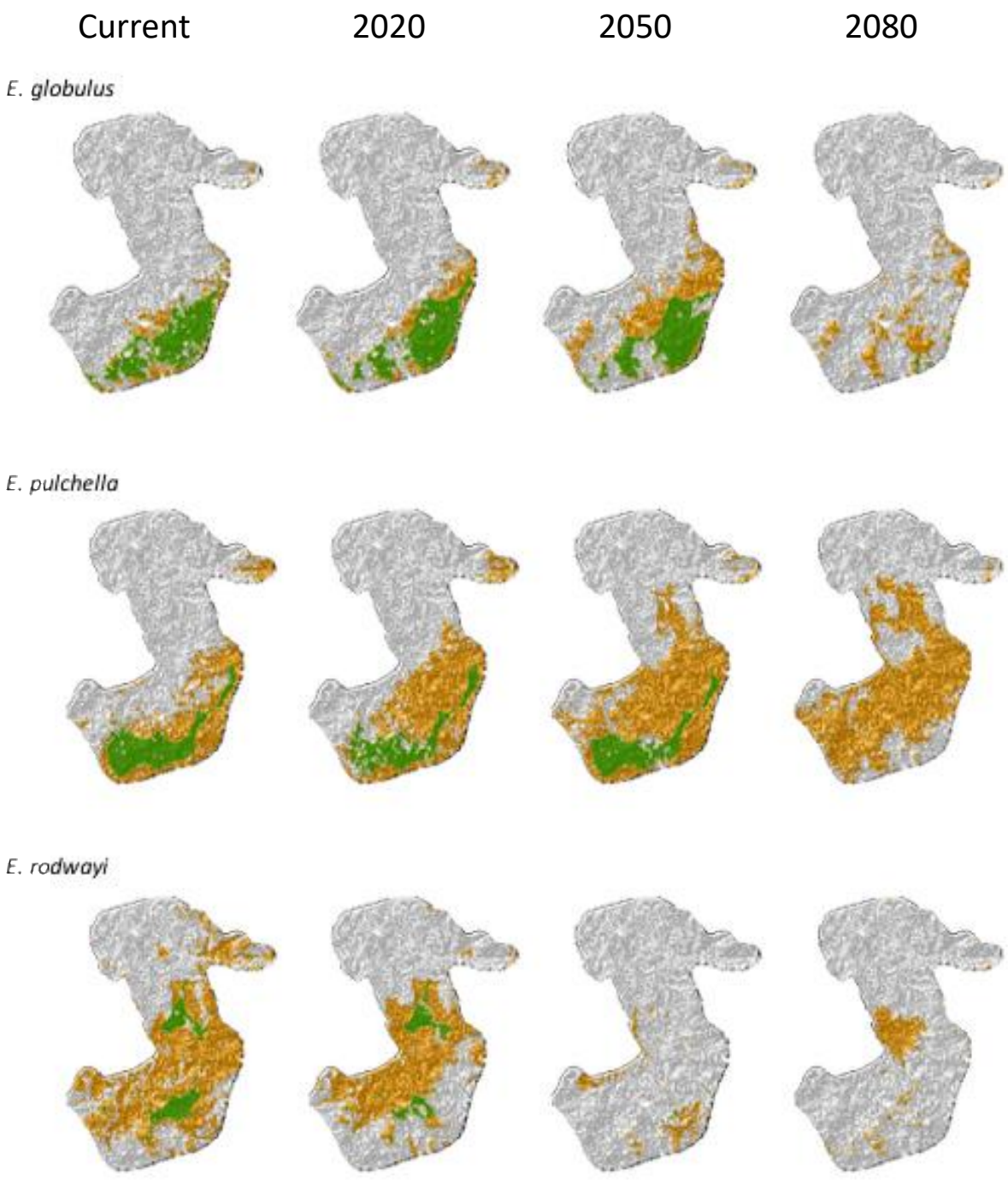
Percent area of the Midlands with predicted suitable habitat within and outside the species convex α-hull. The convex α-hull was calculated by firstly identifying the occurrences within the climate space of the Midlands defined by the first three axes of the PCA (Appendix B7), then spatially confining these occurrences to the geographic extent of the Midlands. The convex α-hull was calculated using an $\alpha = 0.1$ which captured the distribution of these points without over-predicting the species area within the Midlands. The area of suitable habitat within and outside the convex α-hull was calculated by cropping the modelled suitable habitat of a species maintained within the geographic extent of the Midlands region (Figure 3.6; Appendix B9). The area within the convex α-hull represents the area of suitable habitat for a species that has populations local to the Midlands region as well as remaining within the climate space of the Midlands for each mapped point in time. The area outside the convex α-hull represents the area of suitable habitat where no provenance local to the Midlands region were predicted to remain within the climate space of the Midlands for each mapped point in time.

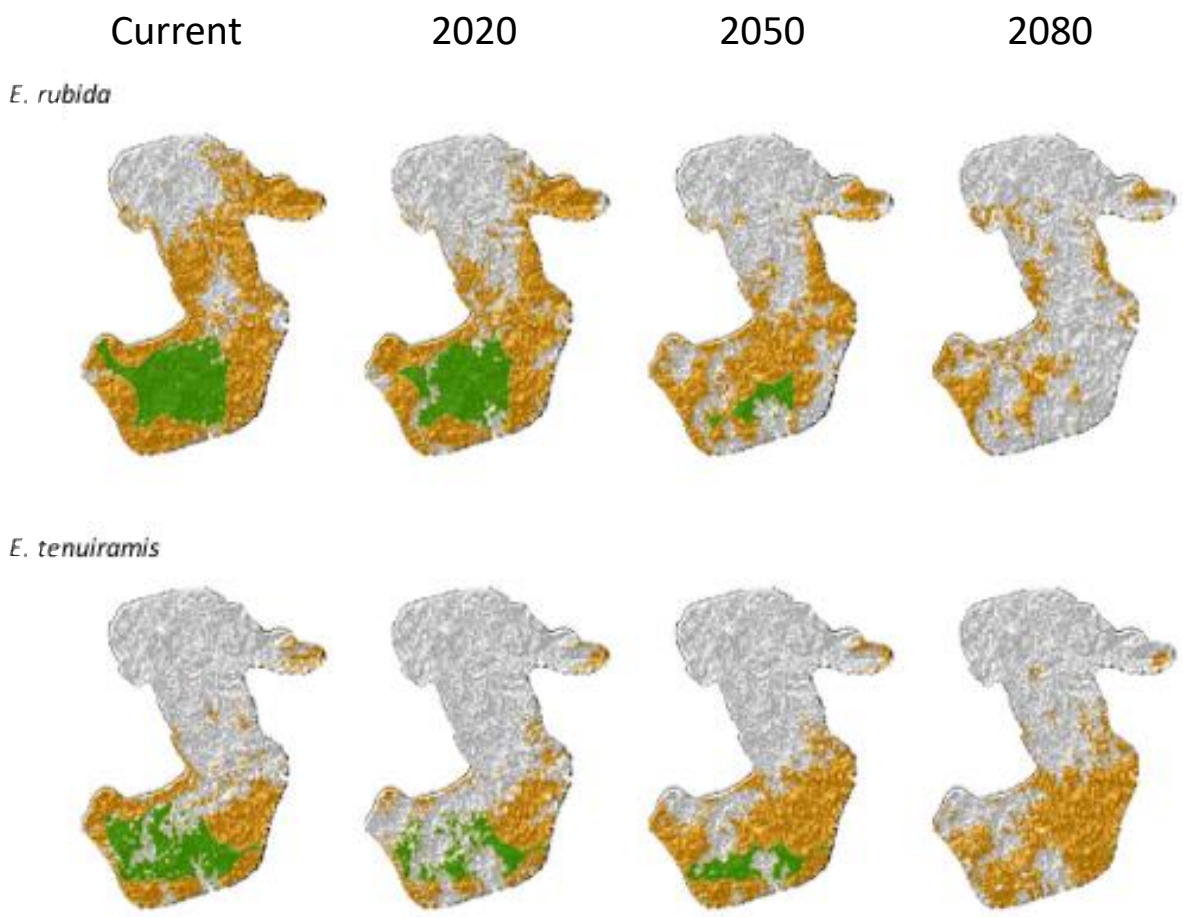
Species	Modelled habitat within α-hull (green surface)				Modelled habitat outside α-hull (orange surface)			
	Current	2020s	2050s	2080s	Current	2020s	2050s	2080s
E. amygdalina	28.6	21.1	21.2	0.9	6.1	6.7	18.4	45.3
E. barberi	0.0	0.0	0.0	0.0	11.6	10.4	15.1	8.7
E. globulus	12.5	12.3	11.5	0.5	5.4	6.9	14.1	9.7
E. ovata	52.1	57.8	46.9	0.8	12.7	17.0	45.5	95.5
E. pauciflora	45.4	30.4	0.2	0.0	29.6	19.4	9.8	0.0
E. pulchella	10.7	9.1	9.0	0.0	18.5	26.4	37.3	45.4
E. risdonii	0.0	0.0	0.0	0.0	6.0	11.3	44.5	55.9
E. rodwayi	6.0	4.6	0.2	0.0	41.9	30.1	4.8	7.0
E. rubida	17.9	15.7	3.9	0.0	51.4	42.5	37.8	20.2
E. tenuiramis	14.7	8.6	5.8	0.1	23.3	16.8	32.4	35.3
E. viminalis	40.3	29.6	22.2	0.4	5.8	8.1	15.6	30.4

Supplementary material B9

The distribution of suitable habitat for each species that had on average > 10% occupation in the Midlands through time (Criteria 1, green and orange surface) and that occupied the current and future climate space of the Midlands (Criteria 2, green surface). The green surface represents areas that are predicted to be suitable habitat for a species and where there are local populations with the climate space of the Midlands. The orange surface represents areas that are predicated to be suitable for the species, but may not have local populations (i) current occurring at these locations or (ii) that are predicted to be outside the current or future climate space of the Midlands. The white/grey surface represents areas that are not suitable for a species under current or future climate conditions of the Midlands.




Current
2020
2050
2080
E. globulus
E. pulchella
E. rodwayi


Current
2020
2050
2080
E. rubida
E. tenuiramis

Appendix C - Supplementary material for Chapter 4

Supplementary material C1

A vignette introducing the PUCA R package to identify distribution records that have analogous climates with the Cressy restoration site.

C1.1 Introduction

This vignette is an introduction to the Provenancing Using Climate Analogues (PUCA) package that implements the operational framework that integrates the climate-adjusted provenancing strategy of Prober *et al*. (2015) with population genetic concepts in the R statistical computing language (R Core Team 2016). The premise of the PUCA package is to use envrionmental data from a restoration region and summaries the main Principal Components (PCs) of variation through this multivariate data cloud. The multivariate space defined by the retained PCs is then used to calculate the dissimilarities between the revegetation site and each distribution record of a species (Figure 1). Here, we demonstrate the graphical user interface (GUI) of the PUCA package for the revegetation site at Cressy (Figure 2). Throughout this vignette, functions and results from the PUCA package will be presented using `Lucida Console` type-face, and executable code will be presented using `Lucida Console` type-face.

C1.2 Prior installation of required R packages

The PUCA package makes use of several R packages, including FactoMineR (Le, Josse & Husson 2008), maptools (Bivand and Lewin-Koh 2015), mefa (Solymos 2009), raster (Hijmans 2015), RJSONIO (Lang 2014), sp (Pebesma and Bivand 2005; Bivand, Pebesma & Gomez-Rubio 2013), tcltk (R Core Team 2014), and tcltk2 (Grosjean 2015). These packages (and associated dependencies) are automatically downloaded when PUCA is first installed.

However, prior to PUCA being installed, there are three separate packages that must be present. These include devtools (Wickham and Chang 2015), ALA4R (Raymond, VanDerWal & Belbin 2015), and rgbif (Chamberlain *et al.* 2015).

The first package to install is devtools. This package facilities the download of ALA4R, rgbif, and PUCA from the GitHub repository using the `install_github` function. The following code chunk will install the devtools package, all of its dependencies and then load it into the global workspace. The subsequent code will then download ALA4R, rgbif and PUCA from GitHub, along with their dependent packages. The last line calls the PUCA library. [Note: this process requires an internet connection and may take a few minutes to run as there are a number of dependent packages that will be downloaded (if not already in the R library folder)].

```
install.packages("devtools", dependencies = TRUE)
library(devtools)
devtools::install_github("AtlasOfLivingAustralia/ALA4R", dependencies =
TRUE)
devtools::install_github("ropensci/rgbif", dependencies = TRUE)
devtools::install_github("peteraharrison/PUCA", dependencies = TRUE)
library(PUCA)
Welcome to PUCA version 1.0!
```

C1.3 The different features of the PUCA GUI

The GUI for the PUCA package can be called by running `seedSource_GUI()`. This will initiate two windows (Figure APP1.1), one with the 'Terms and Conditions' of using the package, and the other is the front-end of the GUI. To use the GUI, the 'Terms and Conditions' must be accepted by clicking 'I AGREE'. The 'Terms and Conditions' outline the GNU General Public Licence (version 3), under which this package is licensed.

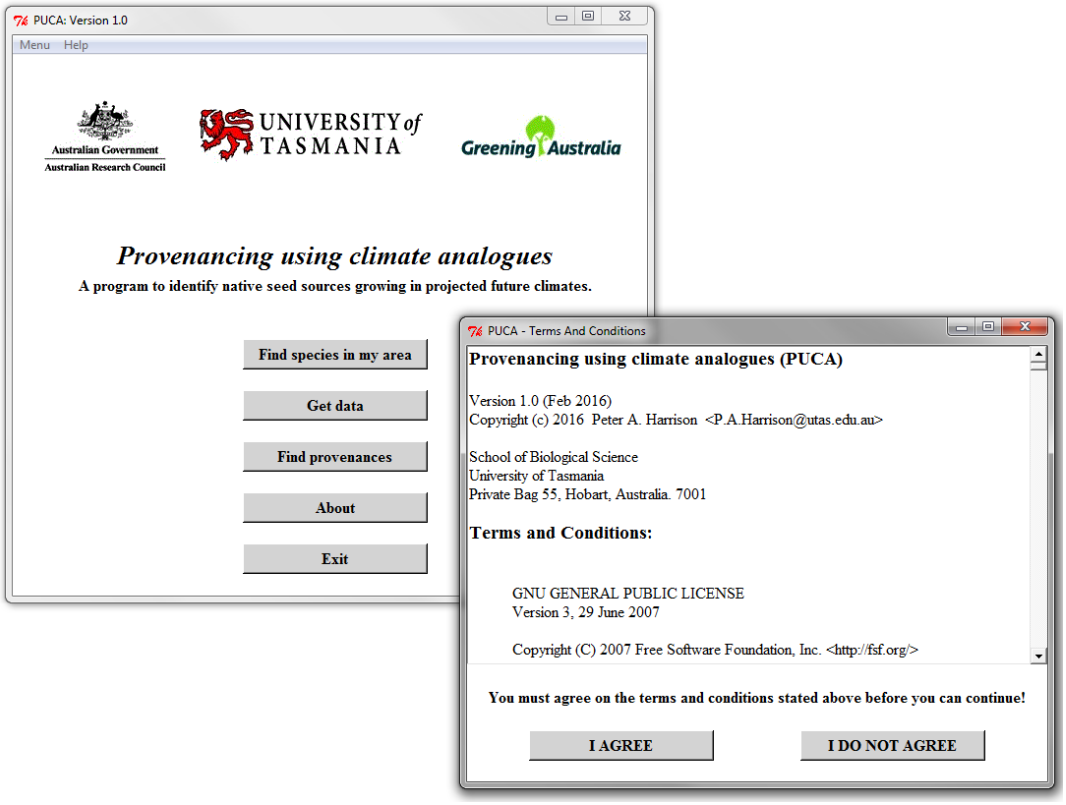


Figure APP1.1 The front-end of the PUCA graphical user interface and the 'Terms and Conditions' for use of the PUCA package.

The front-end of the GUI provides easy access to three core functions:

(i) Find species in my area (Figure APP1.2).

This module allows you to search for what species (both animal and plant) are within a radius *r* of a revegetation site. First a spatial polygon of radius *r* is created, which is then passed to either the Atlas of Living Australia (ALA) or Global Biodiversity Information Facility (GBIF) API servers. Which server this function uses is dependent on the location of the revegetation site. For example, the Cressy revegetation site is in located in Tasmania, Australia, thus it uses the ALA API server. If the revegetation site is outside of Australia, the GBIF API server is used. After clicking 'Find species' a list of species scientific names are returned, which are ordered using the frequency of occurrences within the polygon. Next, a plot of a selected species distribution can be shown by clicking 'Plot distribution'. If you want to download the distribution data (single or multiple species allowed), simply select

from the list by holding 'Ctrl' and clicking each species name individually. Once you have selected the species and click 'Select species and return', the function will download the distribution records and store the data in the global environment as class data.frame, then return to the main screen of the PUCA package. Within this data frame are three variables: the species name (`species`), the latitude (`Latitude`) and longitude (`Longitude`) coordinates for each distribution point. Each species will have the prefix `species_` before its scientific name in the global environment.

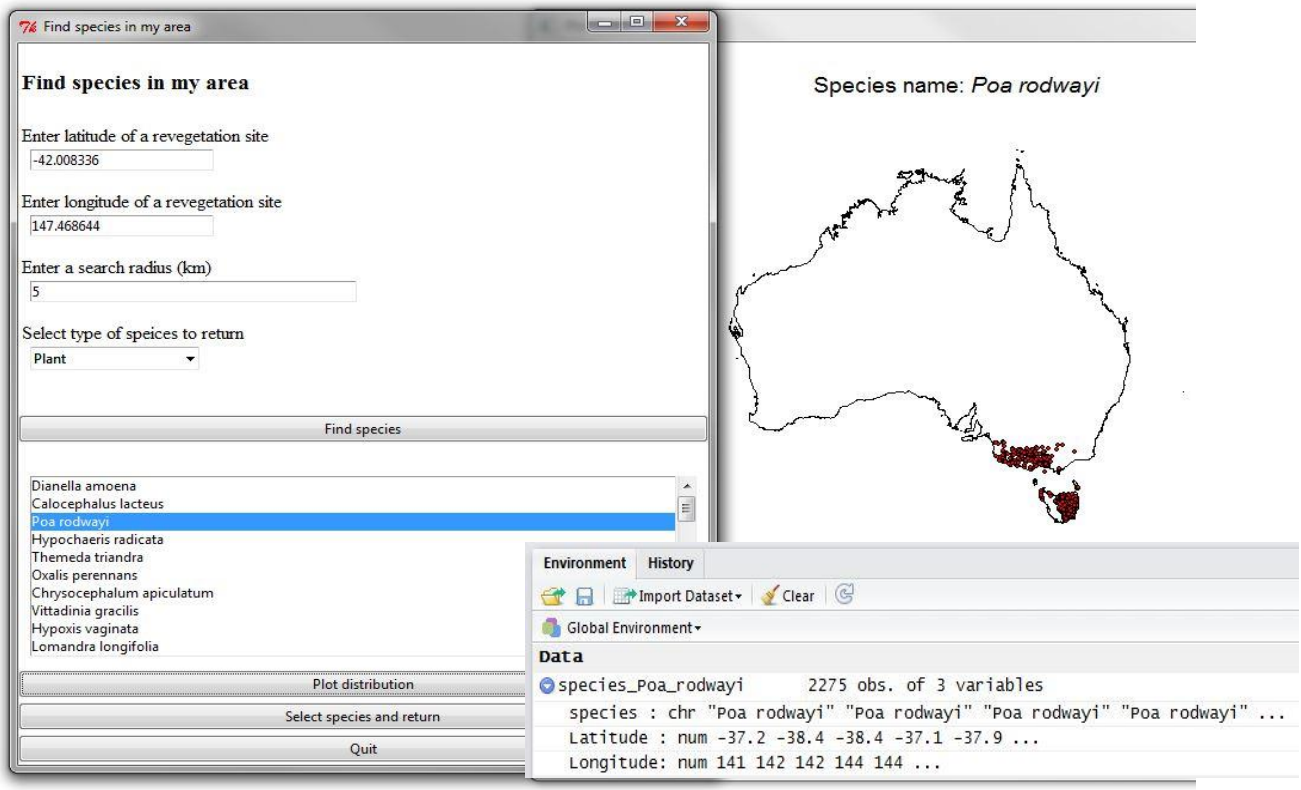


Figure APP1.2 The 'Find species in my area' module, showing the Latitude and Longitude field for a revegetation site, the radius of the polygon field, and a drop down field to specify whether plants, animals, or both should be returned. The plot of *Poa rodwayi* was made by selecting the species from the list and click 'Plot distribution', and clicking 'Select species and return' writes a `data.frame` to the global environment.

(ii) *Get data* (Figure APP1.3; Figure APP1.4).

This function has two options. The first is to allow the user to enter their own species and climate data by using the 'Browse' button to direct R to retrieve the data. There is no limit to the number of species entered, nor are there for the number of future climate projection models. There is, however, an assumption on the names for the different files and folders. For each species, it is assumed the file is a **comma delimited file** (*.csv extension) containing at least three columns matching the following names exactly: **species**, **Latitude**, **Longitude**. If these names are not found an error message will be printed to the console. Further, the lowest nested folder containing the baseline climate data must be named **current**. Similarly, the lowest nested folder containing the future climate data must be unique and contain the global circulation model (GCM) name and year period (specifically, **model_year**). For example, if future projected climate data were stored here C:\climate data\future climate\csiro_2020, csiro_2020 would be the lowest nested folder containing the projected climate for 2020 by the csiro GCM. The number of climate variables for the baseline and future climate must also match. That is, if the baseline climate has 19 bioclimatic variables, then each time slice of the GCM must contain the projected values for the same 19 bioclimatic variables. Presently, the GUI only accepts ASCII files with extension *.asc, other extensions will be supported in later releases of PUCA. [Note: if the climate data is in another format than *.asc, it can be read into R using the raster package.].

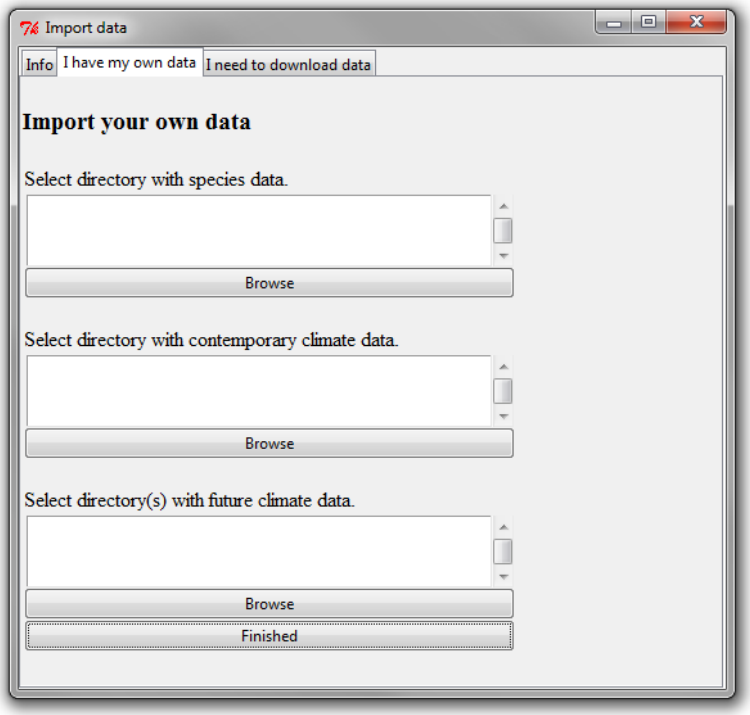


Figure APP1.3 The 'Import your own data' tab of the 'Get data' module. Use the 'Browse' buttons to search for the required files or directories.

The second option is a wrapper function that provides access to the WorldClim data (http://www.worldclim.org/; Hijmans *et al.* 2005) using the getData function of the raster package. The latitude and longitude fields will contain the respective decimal degree coordinates for the revegetation site. The next option is to download the global circulation models (GCMs). Some of the GCMs are only available for non-commercial use and these are indicated by the * symbol. Multiple GCMs can be selected by holding 'Ctrl' and clicking each model individually. Three resolutions (grid cell size) are available, including 2.5 arc minutes (ca. 4.5 km at the equator), 5 arc minutes (ca. 9 km at the equator), 10 arc minutes (ca. 18.5 km at the equator). Finer resolutions are also available (30 arc sec or ca. 1km at the equator), and will be coded in the next release of PUCA. The next step is to select which climate layers to download (minimum, maximum temperature, annual precipitation, or bioclim), the time slice (multiple can be selected by holding 'Ctrl' and clicking each year

period individually), and the emission scenario (see IPCC 2013 for explanation of the RCP scenarios). For the WorldClim climate data, the baseline data is the average of the time period between 1950 and 2000, and the future projection data for the 2050s is the average for 2041 to 2060, and the 2080s is the average for 2061 to 2080. The last field is optional, and allows the climate data to be permanently downloaded to a directory path. If this field is left blank, the data will be downloaded into a temporary folder that will be deleted when the PUCA package is detached. Once all the required fields are entered, clicking the 'Download data' button which will retrieve the requested data.

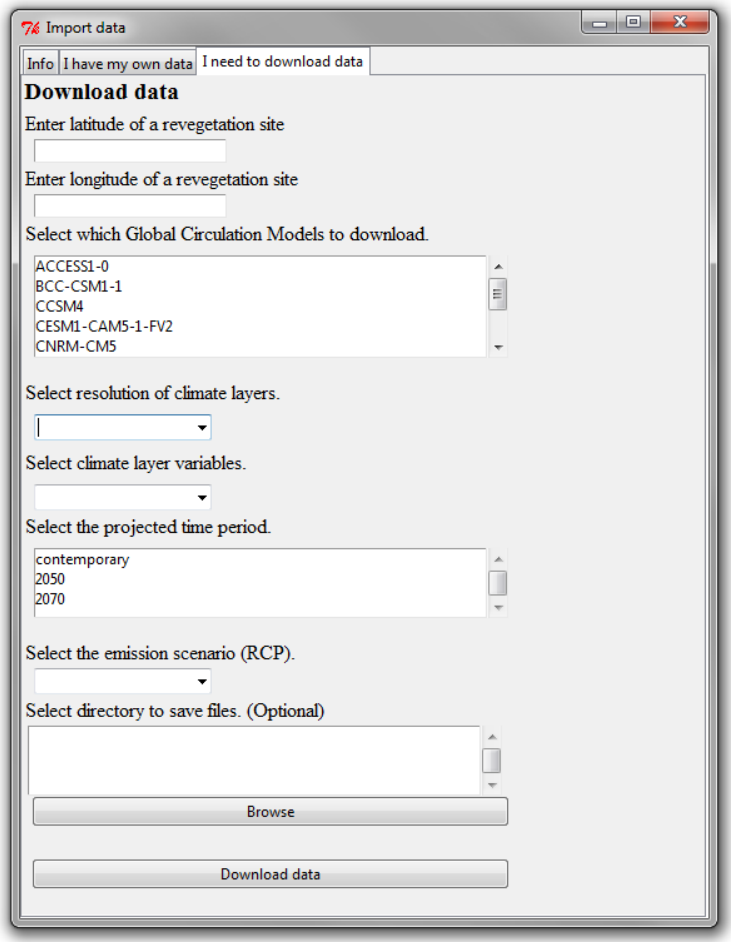


Figure APP1.4 The 'Download data' tab of the 'Get data' module. Shown are the latitude and longitude fields for the revegetation site, the list of global circulation models available to download from WorldClim (see http://www.worldclim.org/; Hijmans *et al.* 2005), the resolution of the climate layers, the climate variables to download, the time slices to

download, the Representative Concentration Pathways (RCP), and a directory to save the download files.

Regardless of how the climate data is entered, albeit using the 'Import your own data' tab or the 'Download data' tab, the climate data will be read into two objects of class RasterStack, and will be named climate_current and climate_future in the global environment.

(iii) Find provenances (Figure APP1.5; Figure APP1.6).

The last module of the PUCA GUI calls the function seedSource to find seed source (hereafter provenances) occurring in baseline and projected analogous bioclimates. This module has two main tabs. The first tab ('Main') lists all the data that was previously entered in the 'Get Data' module. If the data is not listed, then the importing failed and it is recommended to repeat the 'Get Data' module. The first step is to (again) enter in the latitude and longitude coordinates for the revegetation site in decimal degrees. Then, holding 'Ctrl', select which species to use. The last required field to fill in is to select which future GCMs to use. This could be either a single model (i.e. the extreme models) or multiple models. If multiple models are selected, the default action of the `seedSource` function of PUCA is to create a multi-model mean for each time slice.

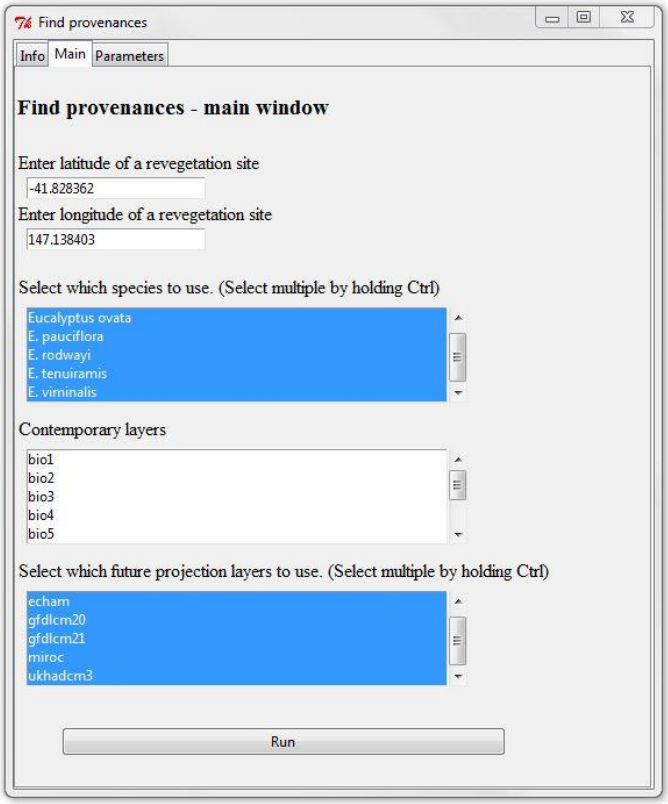


Figure APP1.5 The 'Main window' tab of the 'Find provenances' module, showing the species, baseline climate layers, and the available future projection models.

The second tab ('Parameters') contains the various parameters for the function seedSource. The default values are shown. The first option is to set the restoration field. This option needs careful consideration as it will form the multivariate space that the species (baseline climate) and revegetation site (baseline and future projected bioclimate) are predicted into. By entering a numeric value, the restoration region will be represented by a polygon of radius *r*. In the current study, we used a combination of two bioregions to define the restoration region. In this case, the directory path to the Midlands bioregion was supplied. [Note: it is assumed the revegetation site is located within the defined restoration region.] The next parameter is the size of the buffer around the revegetation site. The aim of the buffer is to increase the sampling size of the revegetation site by creating a polygon of radius *r*. Bioclimatic data is extracted from a uniform grid (usually 20 equal-distance points) within this buffer, with the Standardised Euclidean Distance (SED) calculated between each

distribution record of a species and each point within the buffer. The SED is then transformed into binary using a threshold value. In our current study we used a 2-unit threshold, where points where considered occupying analogous climates if the SED was less than or equal to 2-units. However, if the threshold equals zero, the transformation threshold will automatically calculate the threshold for each species using the mean dissimilarity values for distribution points within 15 km of the revegetation site. This assumes the species is local to the site. If the species is not local, then an error will be produced. The last two options define the number of 'best' matches to print to the console, and a logical indicator (`TRUE`/`FALSE`) of whether to log the progress of the `seedSource` function as it runs.

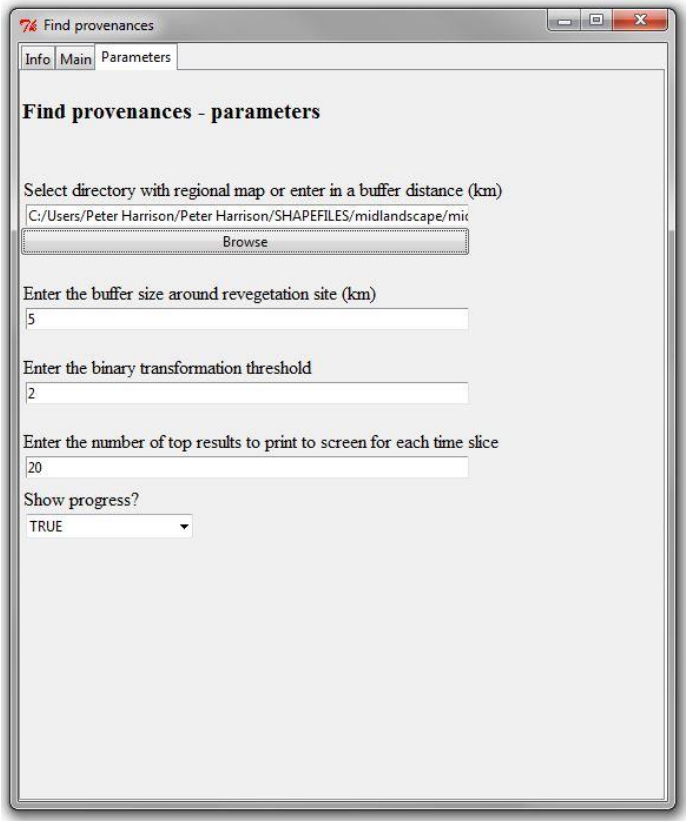


Figure APP1.5 The 'Parameters' tab of the 'Find provenances' module, showing the field to define the restoration region, and the default settings for the buffer size, binary transform threshold, and verbose progress of the seedSource function.

C1.4 Using the GUI to find provenances analogous to Cressy

We used the revegetation site at Cressy to demonstrate the GUI application of the seedSource function. Here, we used the same bioclimatic layers, species, and parameter settings (Figure APP1.5 and APP1.6) as described in the Material and methods. After clicking the 'Run' button, a log window will appear (Figure APP1.7). This window tracks the progress of the function and reports any errors encountered. Also printed to the screen is the top *x* most analogous provenances, where *x* is depended on the value entered in the field for results to print to screen in the 'Parameters' tab (Figure APP1.7). By default, the top 20 results are printed, and are ordered using the 'climDist' field, which is the SED between that point and the revegetation site in the multidimensional space defined by the restoration region. Also printed is the 'collect' variable which is the binary transformation of the 'climDist' variable based on the binary transformation threshold. The 'geoDist' variable is the geographic distance between that point and the revegetation site calculated using the Great Circle (Haversine) formula. For each species, the Principal Component Analysis is returned to the global environment with prefix '`PCA_`'. Additionally, the results for each time slice will be returned to the global environment with prefix '`output_`' and will be the same length as the number of distribution points entered. [Note: at the end of the function, a warning message may appear stating missing values were imputed using the mean. This message may appear if some distribution points are located outside the coverage of the bioclimatic rasters, i.e. on the coast line. This is generally not an issue if the number of points imputed is small, but it is recommended to either relocate these points half the size of a grid cell away from the coast (i.e. if the resolution is 0.008, then move points 400m from the coast line to still be in the same grid cell). Alternatively, remove that point from the analysis].

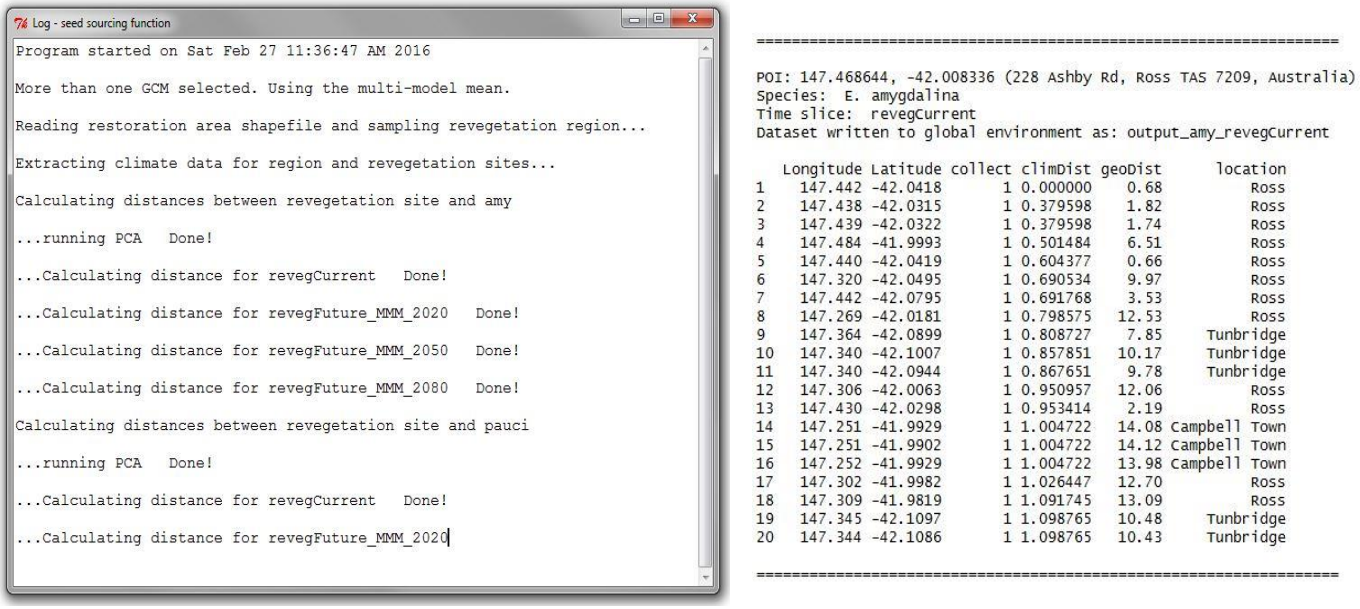


Figure APP1.7 The log window and console output for the function seedSource of the PUCA package.

The typical run time for our analysis took 66 minutes on a Dell Latitude E5420 laptop with an Intel(r) i5-2430M CPU @ 240GHz processor, running a 64-bit Windows 7 operating system. However, the run time will be dependent on how many GCMs are used and the number of distribution points of a species that are read. Once the function is finished, we can (i) determine how many points where `collect = 1` occur in fragmented landscapes, and (ii) plot the density probability function for where `collect = 1`.

The number of points which occur in fragmented landscapes is an important metric as it flags potential sites that may be affected by small population effects (i.e. reduced genetic diversity, increased inbreeding, reduced seed set) (Broadhurst *et al*. 2008; Broadhurst *et al*. 2015; Ellstrand and Elam 1993; Young, Boyle & Brown 1996). To assist, an additional vignette on how to create a habitat fragmentation layer and how to use it to identify and flag

points in fragmented landscapes is available within the PUCA package by calling `vignette("How-to-create-fragmentation-layers", package = "PUCA")`.

To plot the density probability function for where `collect = 1`, we provide a simple plotting function which is available in Appendix S2. This function will create individual plots that can be saved for post-processing in external packages such as Adobe Illustrator. The output for the Cressy revegetation site, along with per cent of analogous points in fragmented landscapes is given in Figure APP1.8.

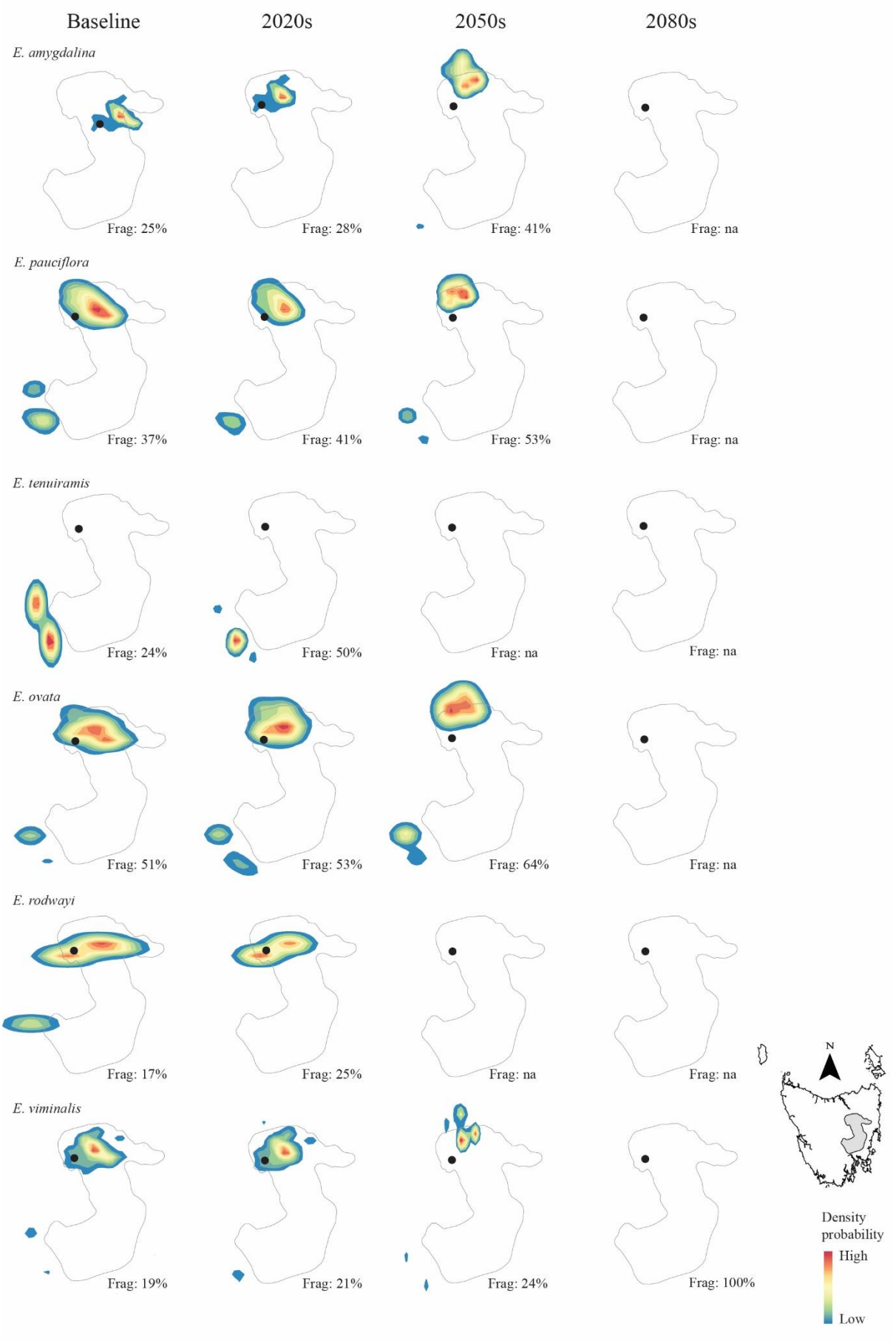

Baseline
2020s
2050s
2080s
E. amygdalina
Frag: 25%
Frag: 28%
Frag: 41%
Frag: na
E. pauciflora
Frag: 37%
Frag: 41%
Frag: 53%
Frag: na
E. tenuiramis
Frag: 24%
Frag: 50%
Frag: na
Frag: na
E. ovata
Frag: 51%
Frag: 53%
Frag: 64%
Frag: na
E. rodwayi
Frag: 17%
Frag: 25%
Frag: na
Frag: na
E. viminalis
Frag: 19%
Frag: 21%
Frag: 24%
Frag: 100%
N
Density probability
High
Low

Figure APP1.8 (page 279) The density probability function for each species climatically matched to the Cressy revegetation site (black dot) for the baseline climate (1976-2005) and the projected multi-model mean climates for the 2020s, 2050s, and 2080s under the A2 emission scenario. The colour ramp corresponds to the smoothed kernel density probability where hot colours represent higher density of climatically matched distribution points. Also shown is the per cent of climatically matched points that were within fragmented landscapes.

C1.5 References

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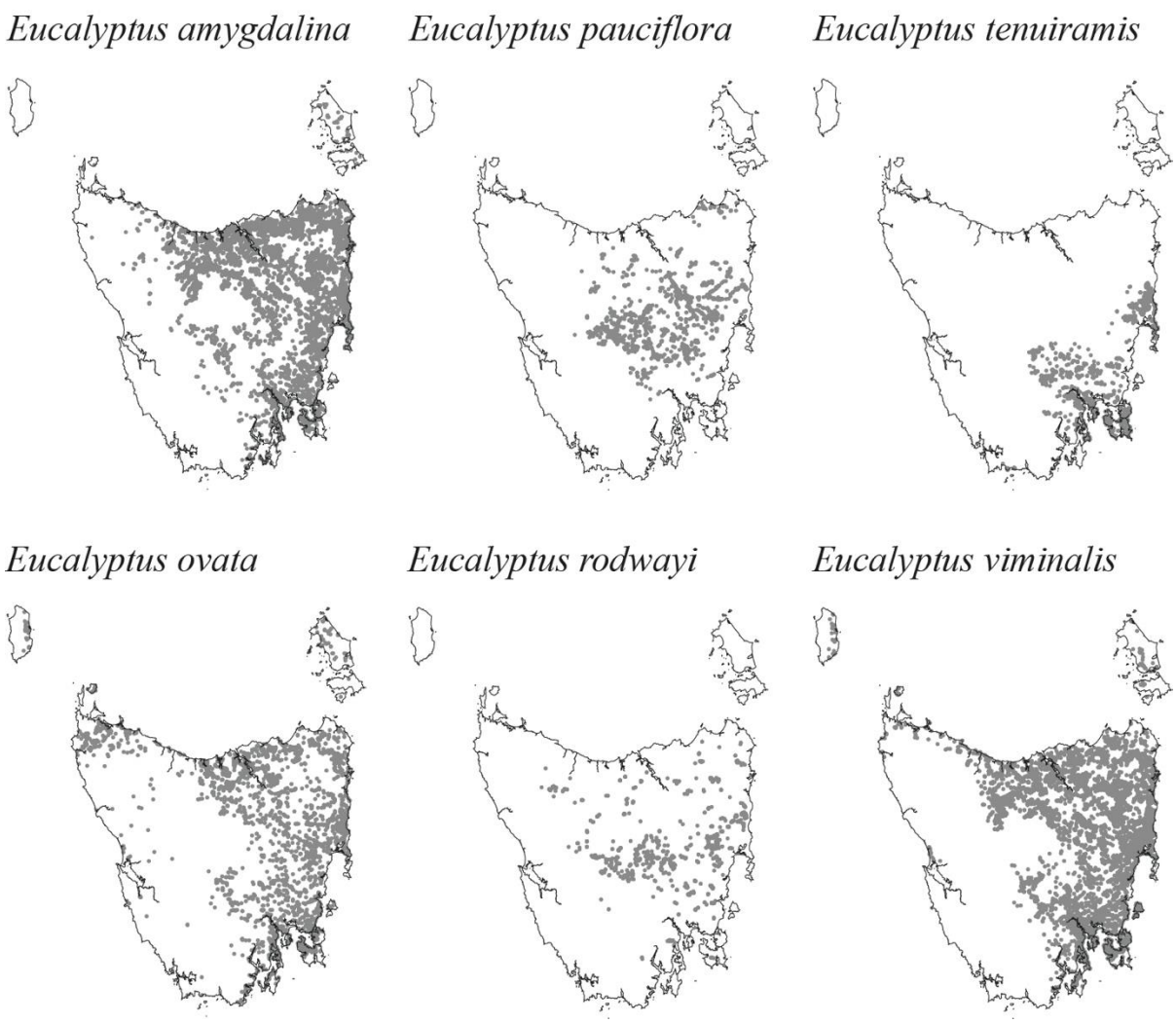
Supplementary material C2

The natural distributions of the three Tasmanian endemic (*Eucalyptus rodwayi*, *E. amygdalina*, and *E. tenuiramis*) and three non-endemic (*E. ovata*, *E. viminalis*, and *E. pauciflora*) eucalypt species (grey circles) used in the current study. Distribution points were obtained from the Natural Values Atlas (https://www.naturalvaluesatlas.tas.gov.au/; accessed 2nd January 2015), with duplicate points and points within 100m of another point were removed.



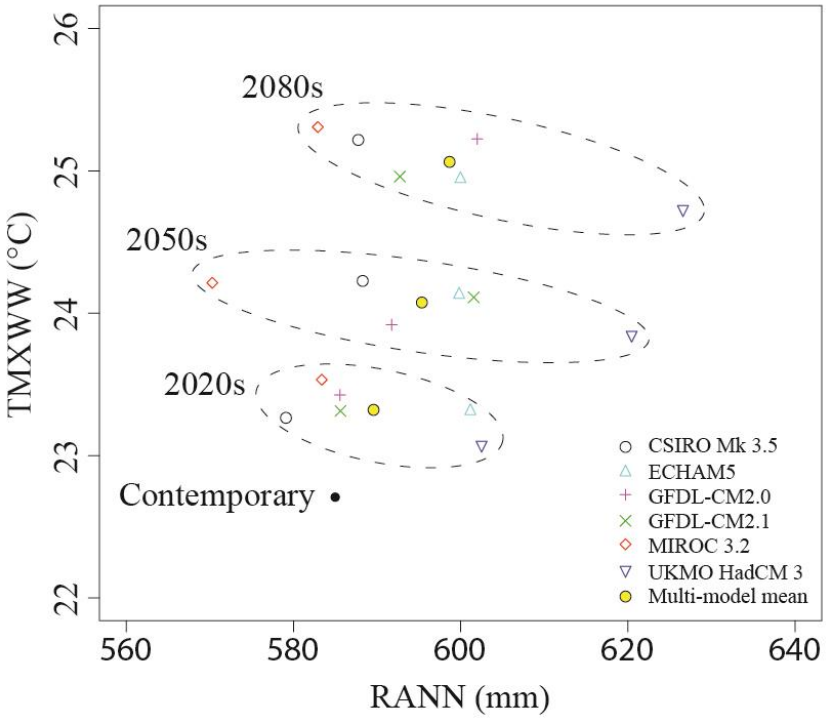
Supplementary material C3

The 11 temperature and 8 precipitation bioclimatic variables and the 8 topographic features used to characterise the climate profile of the Midlands, Tasmania. Shown are the range of values and standard deviation (sd) for each bioclimatic variable using the baseline (1976-2005) climate of the Midlands region, and the mean difference and standard deviation (sd) between the baseline and 2080s projected multi-model mean of six Global Circulation Models for the A2 emission scenario. Also shown are the PCA loadings for each variable, with bold face text representing those variables used to characterise the PC axis.

Variable	Definition	Baseline (sd)	2080s (sd)	PC1 (50.6 %)	PC2 (27.4 %)	PC3 (13.2 %)
TANN	Annual Mean Temperature (°C)	7.5 - 12.4 (0.8)	2.5 (1.6)	0.80	0.13	0.58
TMDR	Mean Diurnal Range	8.6 - 12.4 (0.8)	-0.1 (1.6)	0.89	0.35	-0.21
TIT	Isothermality (TMDR/TSPAN)	0.5 - 0.5 (0.0)	0.0 (0.0)	0.87	-0.08	0.08
TCVAR	Temperature Seasonality	1.1 - 1.4 (0.1)	0.0 (0.1)	0.79	0.50	-0.28
TMXWW	Max Temperature of Warmest Week (°C)	18.0 - 24.7 (1.3)	2.4 (2.6)	**0.92**	0.33	0.12
TMNCW	Min Temperature of Coldest Week (°C)	-0.5 - 2.8 (0.5)	2.3 (1.1)	0.02 ns	-0.30	**0.94**
TSPAN	Temperature Annual Range (°C)	17.7 - 23.8 (1.4)	0.0 (2.7)	0.85	0.42	-0.25
TWETQ	Mean Temperature of Wettest Quarter (°C)	3.9 - 15.1 (2.4)	2.3 (4.8)	-0.06	**-0.82**	0.26
TDRYQ	Mean Temperature of Driest Quarter (°C)	4.6 - 16.2 (3.1)	2.5 (5.8)	0.32	0.64	0.12
TWMQ	Mean Temperature of Warmest Quarter (°C)	11.6 - 16.8 (0.9)	2.7 (1.9)	0.87	0.25	0.42
TCLQ	Mean Temperature of Coldest Quarter (°C)	3.5 - 8.0 (0.7)	2.4 (1.3)	0.64	-0.02 ns	0.76
RANN	Annual Precipitation (mm)	444 - 1168 (75)	14 (156)	-0.74	0.64	0.17
RWETW	Precipitation of Wettest Week (mm)	10 - 35 (3)	1 (6)	-0.49	0.84	0.16
RDRYW	Precipitation of Driest Week (mm)	5 - 13 (1)	0 (2)	**-0.93**	0.08	0.16
RCVAR	Precipitation Seasonality	11 - 29 (3)	1 (6)	0.18	0.88	0.01 ns
RWETQ	Precipitation of Wettest Quarter (mm)	125 - 379 (27)	4 (57)	-0.57	0.80	0.11
RDRYQ	Precipitation of Driest Quarter (mm)	97 - 2064 (14)	3 (28)	-0.92	0.18	0.19
RWMQ	Precipitation of Warmest Quarter (mm)	104 - 2251 (15)	2 (31)	-0.93	0.03 ns	0.26
RCLQ	Precipitation of Coldest Quarter (mm)	109 - 371 (30)	7 (66)	-0.49	**0.84**	0.16

Supplementary material C4

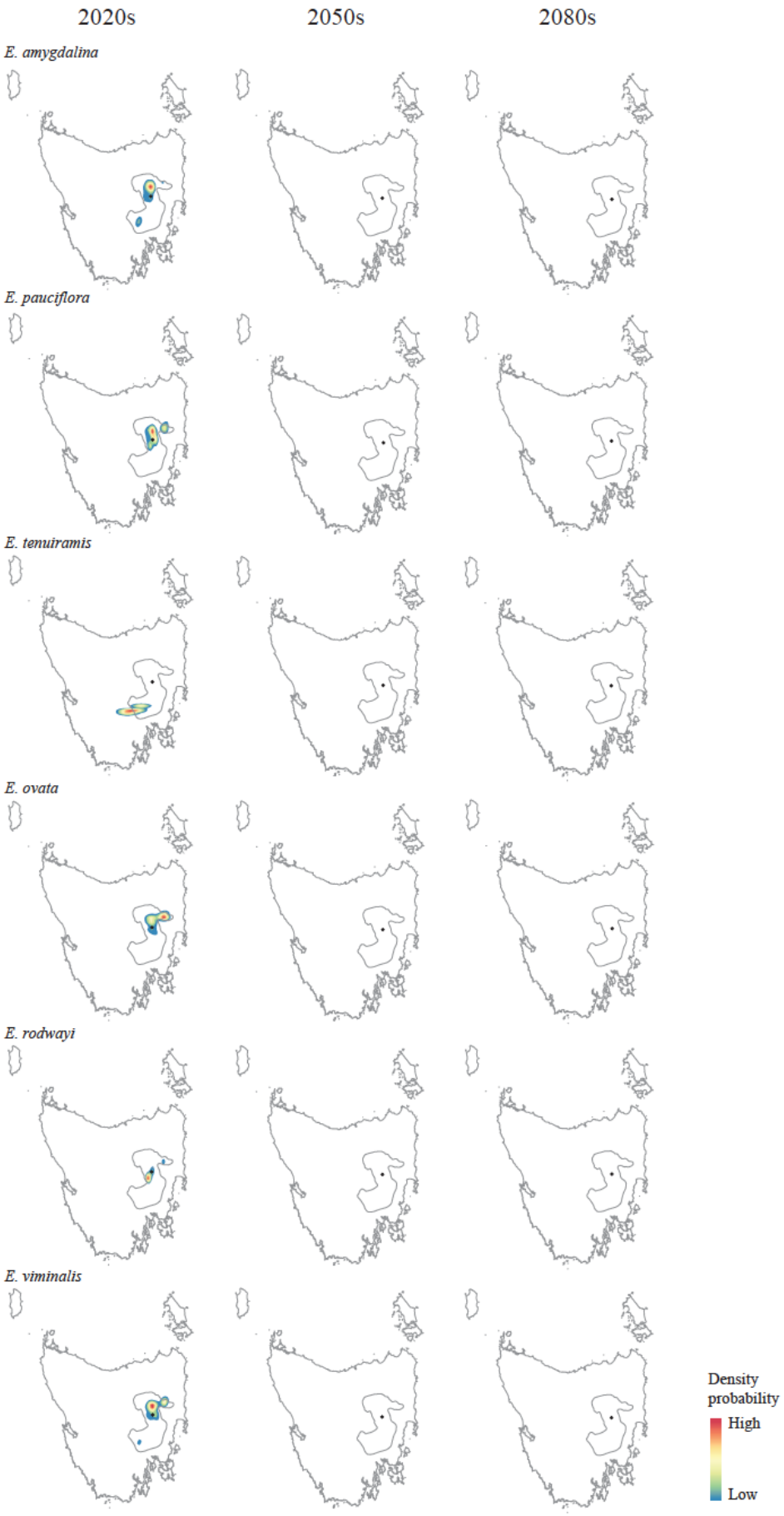
The range of values for the mean annual precipitation (RANN) and temperature of the warmest week (TMXWW) for the Midlands region projected by six Global Circulation Models (GCMs). The means were calculated for the baseline climate (1976-2005), 2020s, 2050s, and 2080s under the A2 emission scenario. Also shown is the multi-model mean used in the current study for the Midlands relative to the six GCMs.

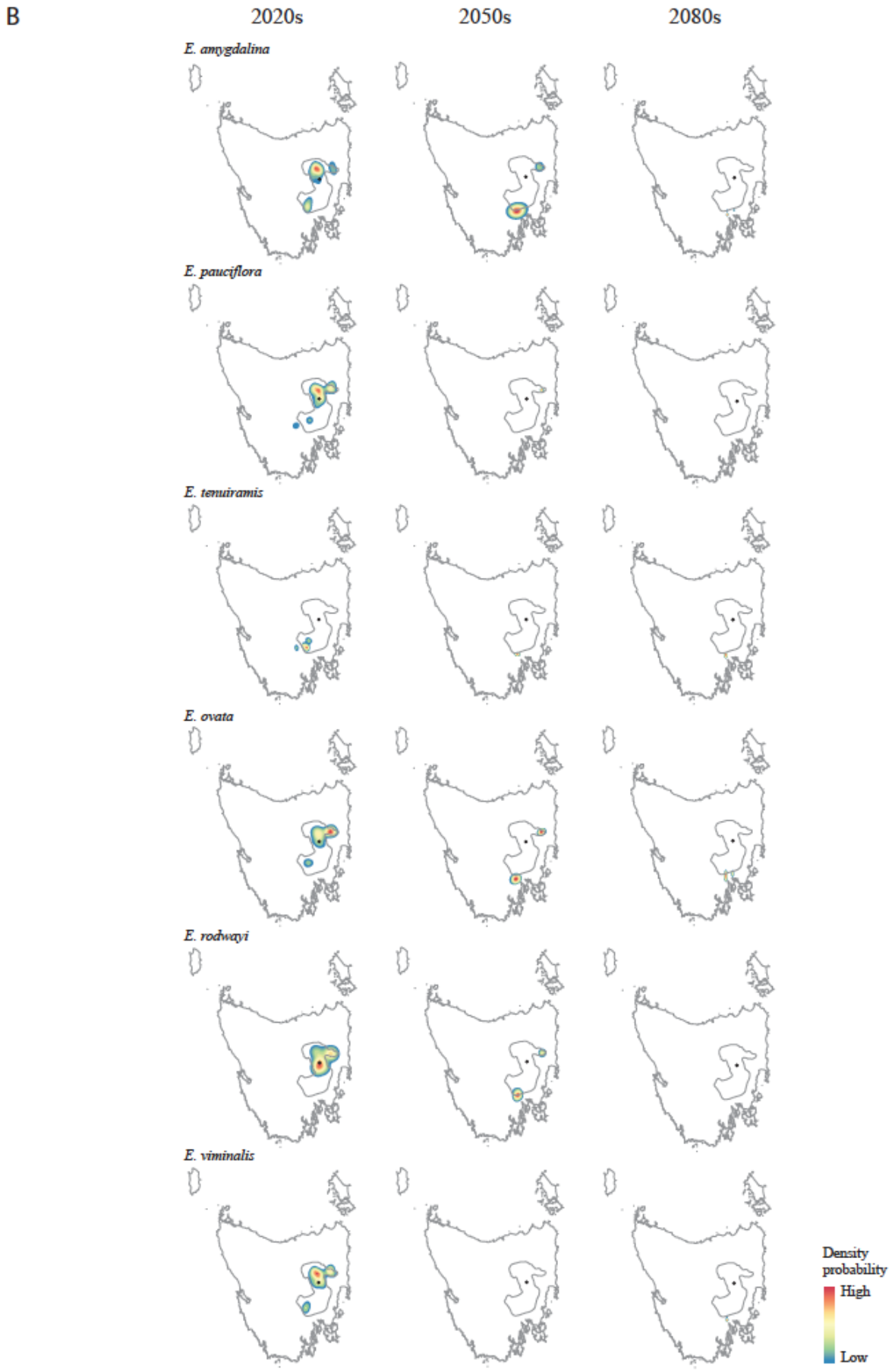


Supplementary material C5

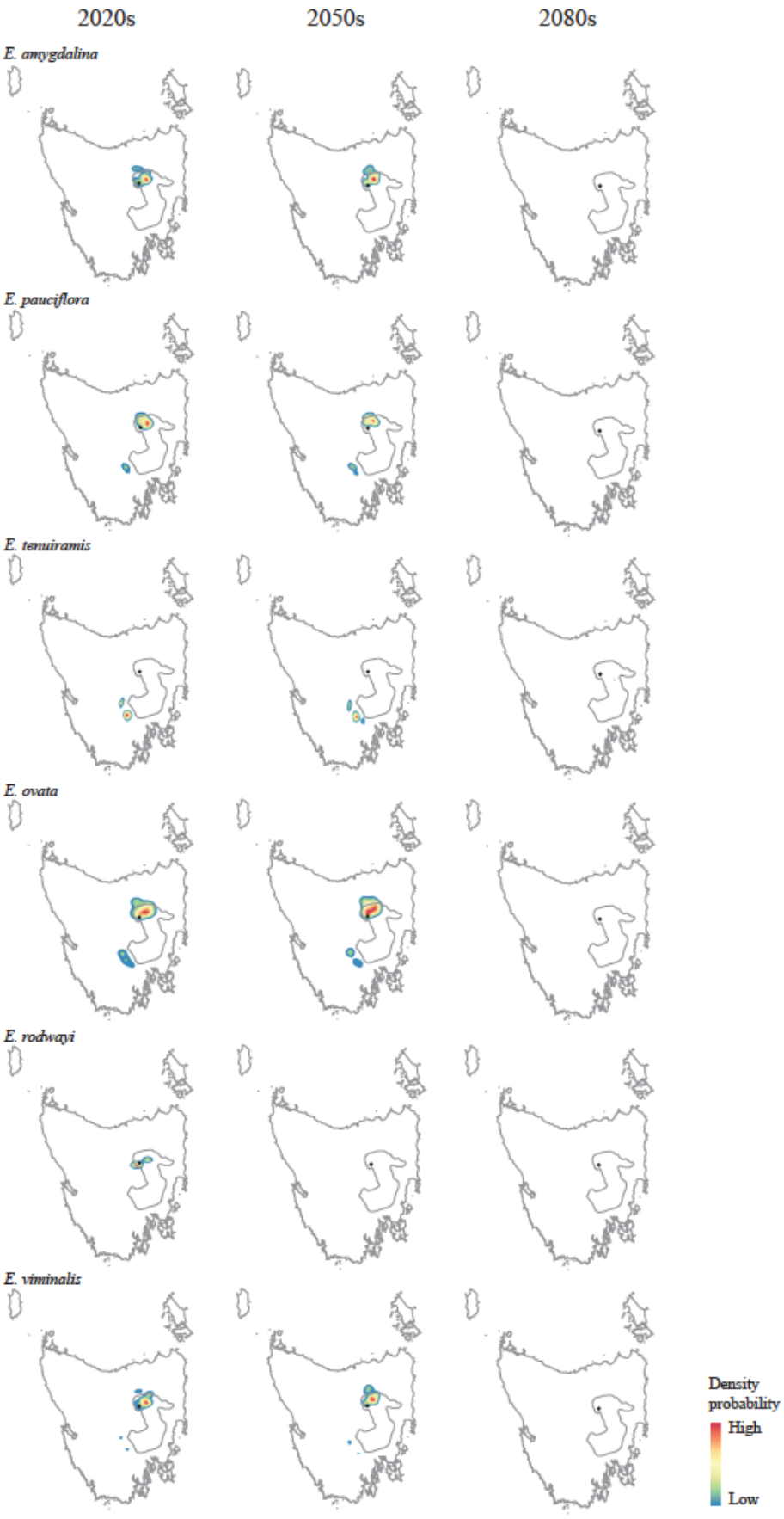
The density probability function for each species climatically matched to the Ross (A and B) and Cressy (C and D) restoration site (black dot) for the projected climates of the 2020s, 2050s, and 2080s under the A2 emission scenario for the two extreme models (MIROC 3.2 (medres) [A and C] and UKMO HadCM 3 [B and D]) from S5. The colour ramp corresponds to the smoothed kernel density probability where hot colours represent higher density of distribution points occurring in analogous climates projected for the restoration site.

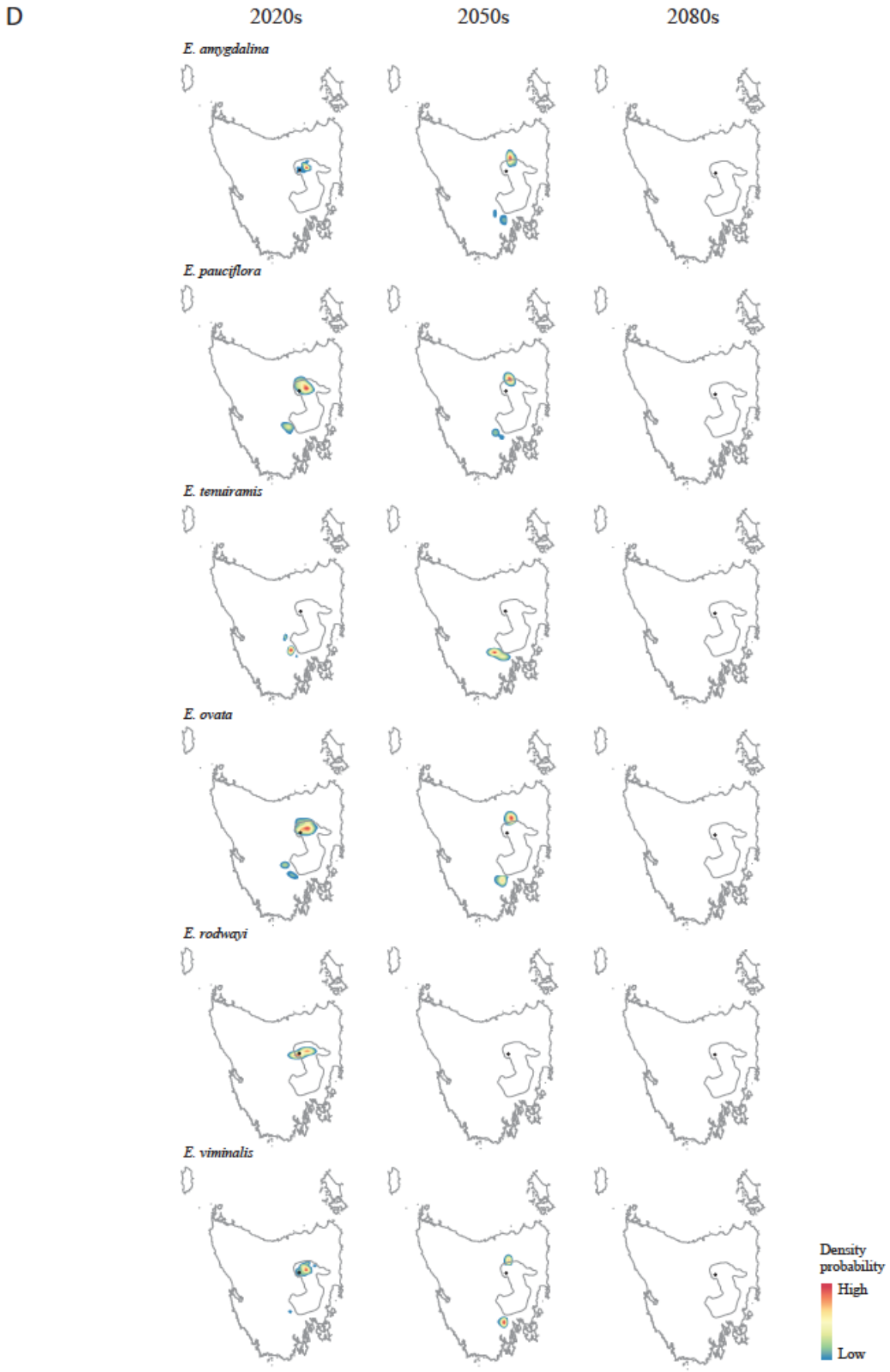
A


2020s
2050s
2080s
E. amygdalina
E. pauciflora
E. tenuiramis
E. ovata
E. rodwayi
E. viminalis
Density probability
High
Low


B
2020s
2050s
2080s
E. amygdalina
E. pauciflora
E. tenuiramis
E. ovata
E. rodwayi
E. viminalis
Density probability
High
Low

C


2020s
2050s
2080s
E. amygdalina
E. pauciflora
E. tenuiramis
E. ovata
E. rodwayi
E. viminalis
Density probability
High
Low


D
2020s
2050s
2080s
E. amygdalina
E. pauciflora
E. tenuiramis
E. ovata
E. rodwayi
E. viminalis
Density probability
High
Low

Appendix D - Supplementary material for Chapter 6

Supplementary material D1

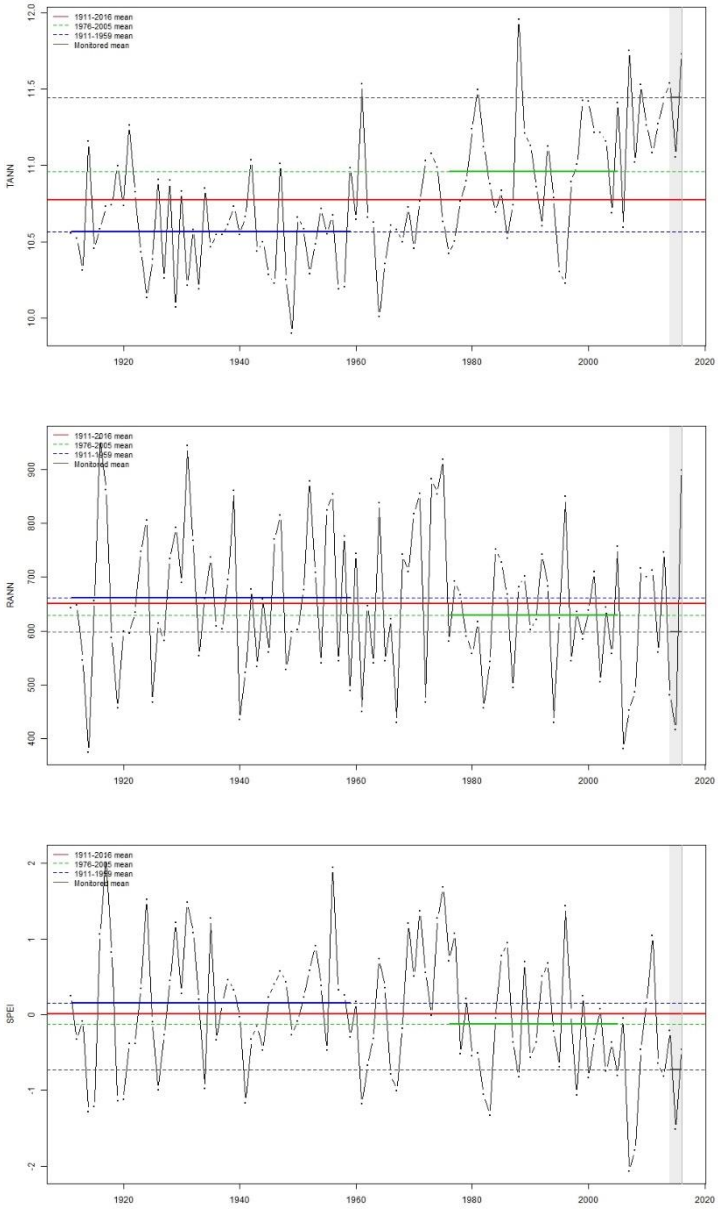
Temperature, precipitation, and radiation bioclimatic variables calculated using ANUClim version 6.1. Shown is the code for each bioclimatic variable, the grand mean and upper and lower 95% confidence interval (CI) for 2185 observations of *Eucalyptus ovata* in eastern Tasmania.

Climate variable	Code	Mean	Lower CI	Upper CI
Temperature				
Annual Mean Temperature	TANN	11.5	8.9	13.3
Mean Diurnal Range *	TMDR	9.7	7.5	12.1
Isothermality	TIT	0.5	0.5	0.5
Temperature Seasonality **	TCVAR	1.1	0.9	1.3
Max Temperature of Warmest Period	TMXWW	21.9	19.5	24.3
Min Temperature of Coldest Period	TMNCW	2.7	0.2	5.5
Temperature Annual Range	TSPAN	19.2	15.0	23.3
Mean Temperature of Wettest Quarter	TWETQ	9.8	5.7	15.6
Mean Temperature of Driest Quarter	TDRYQ	13.5	7.1	17.0
Mean Temperature of Warmest Quarter	TWMQ	15.6	13.1	17.1
Mean Temperature of Coldest Quarter	TCLQ	7.5	4.8	9.7
Precipitation				
Annual Precipitation	RANN	779.5	512.3	1135.2
Precipitation of Wettest Period	RWETW	21.1	12.2	35.1
Precipitation of Driest Period	RDRYW	9.2	6.4	14.0
Precipitation Seasonality **	RCVAR	19.7	11.1	33.7
Precipitation of Wettest Quarter	RWETQ	244.1	148.8	396.5
Precipitation of Driest Quarter	RDRYQ	149.9	107.0	226.0
Precipitation of Warmest Quarter	RWMQ	159.0	118.4	236.9
Precipitation of Coldest Quarter	RCLQ	230.5	126.3	394.5
Radiation				
Annual Mean Radiation	RRANN	13.6	12.6	14.3
Highest Period Radiation	RRH	22.9	21.2	24.0
Lowest Period Radiation	RRL	4.7	4.1	5.1
Radiation Seasonality **	RRCVAR	48.5	45.4	51.7
Radiation of Wettest Quarter	RRWETQ	11.8	6.0	21.6
Radiation of Driest Quarter	RRDRYQ	15.0	6.0	20.8
Radiation of Warmest Quarter	RRWMQ	20.7	19.1	22.1
Radiation of Coldest Quarter	RRCLQ	6.4	5.6	7.0

* Mean diurnal range was calculated as the mean difference between all weekly (n = 52) TMXWW and TMNCW

** Seasonality measures were calculated using the coefficient of variation

Supplementary material D2



Yearly mean climate of the trial site at Cressy over the 1911 to 2016 period. Daily climate data was downloaded from The Australian Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/, accessed 1st March 2017; Jones *et al.* 2009). The daily data was used to calculate (a) mean annual temperature, (b) mean annual precipitation, and (c) the standardised precipitation-evapotranspiration index (SPEI; Vincente-Serrano *et al.* 2010) for each year. The solid black line represents the trend in the data. Four averages were calculated: (i) the grand-mean across the 106 year period (red line), (ii) the mean during the time period (1911-1959) before the detection of anthropogenic climate change in the Southern Hemisphere (Abram *et al.* 2016) (blue line), (iii) the mean during the time period (1976-2005) considered as the baseline contemporary climate (Xu and Hutchinson 2012) (green line), (iv) the mean climate since the commencement of trial at Cressy (grey line and grey vertical shading).

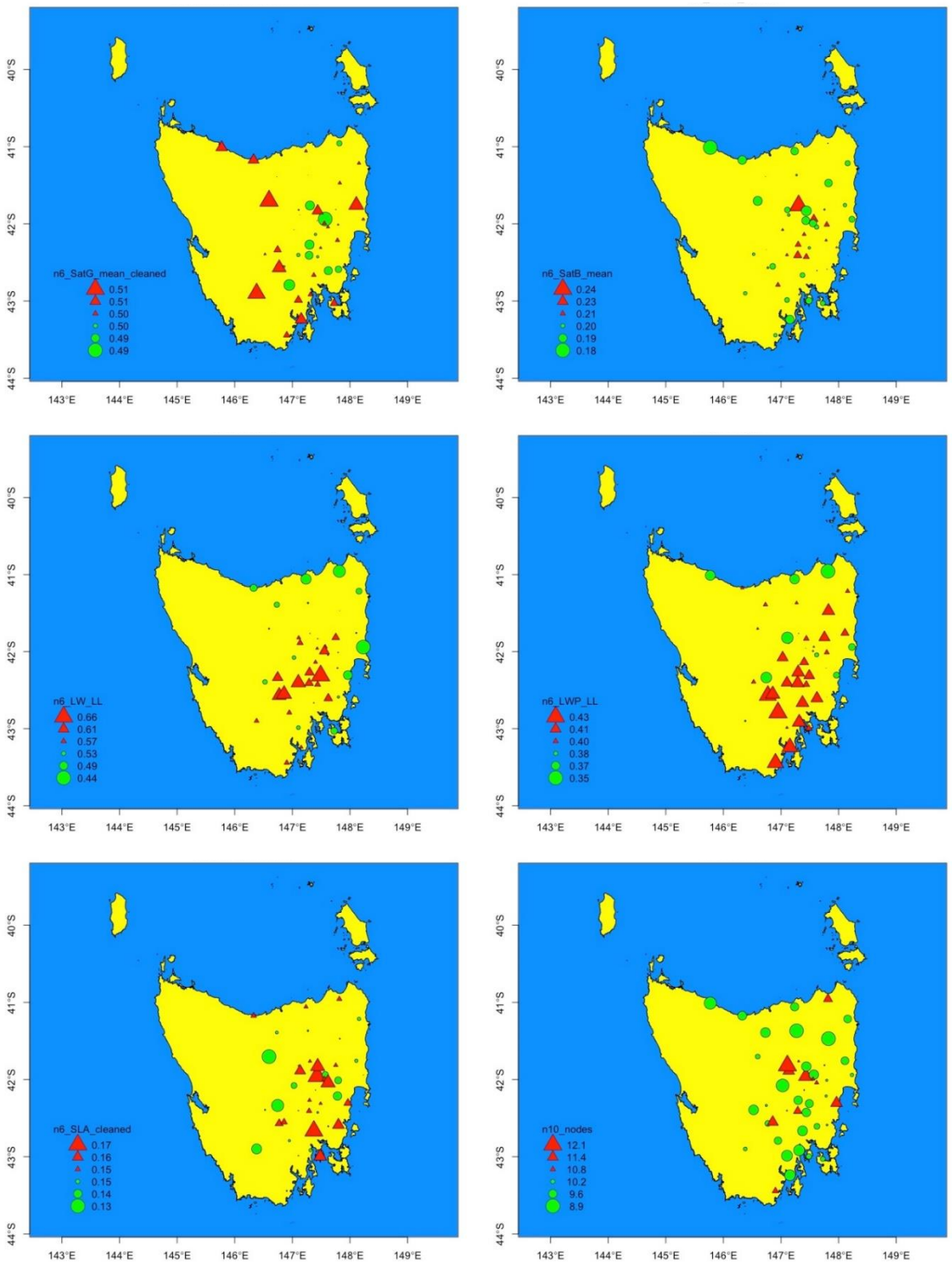
Supplementary material D3

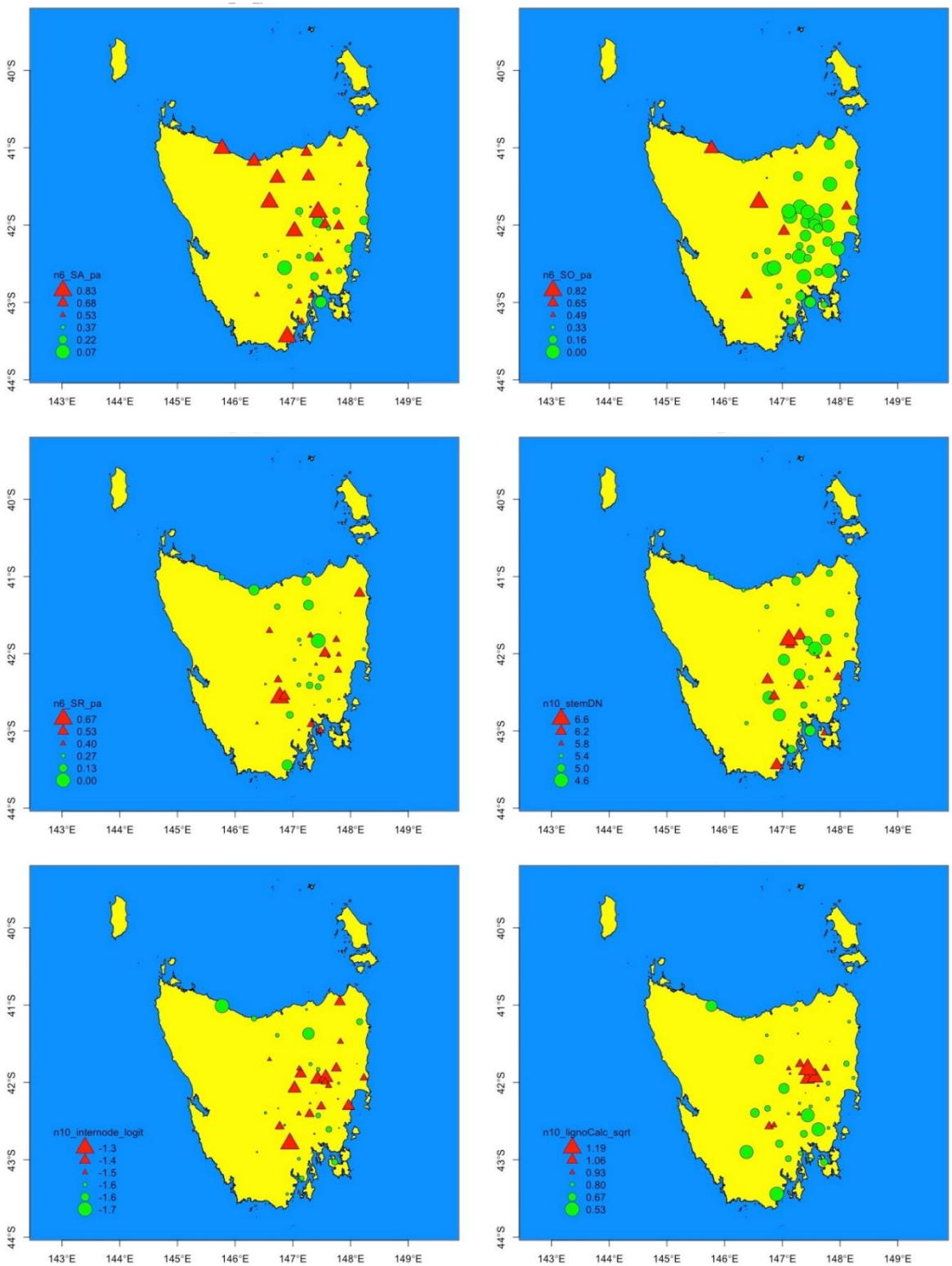
Mean climate of the trial site at Cressy over the contemporary baseline ($Mean_{1976\text{-}2005)}$ period, the mean climate during the growth period ($Mean_{GP}$), and the difference between these two periods (Δ_{diff}). Daily climate data was downloaded from The Australian Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/, accessed 1st March 2017; Jones *et al.* 2009). The daily data was used to calculate the variables listed, and a time-series regression of the yearly trend undertaken using the 'tslm' function of the *forecast* package (Hyndman and Khandakar 2008) in R, showing the year coefficient and its standard error (Yearly trend (± SE)) from the time-series regression and the significant of this yearly trend.

Variable	Description	$Mean_{1976\text{-}2005}$	$Mean_{GP}$	Δ_{diff}	Yearly trend (± SE)	$F_{1,104}$
Mean annual temperature (°C)	The annual average difference in minimum and maximum daily temperature, averaged over a period (e.g. 1976-2005)	11.0	11.4	0.5	0.01 (0.001)	39.2 ***
Maximum temperature of the warmest week (°C)	The absolute maximum daily temperature of the warmest week in a year, averaged over a period (e.g. 1976-2005)	31.3	33.1	1.8	0.02 (0.01)	4.4 *
Minimum temperature of the coldest week (°C)	The absolute minimum daily temperature of the coldest week in a year, averaged over a period (e.g. 1976-2005)	-4.3	-3.8	0.6	-0.002 (0.004)	0.3 ns
Frost days	The number of days in a year with minimum temperatures below 0 °C	50	49	-1	-0.01 (0.03)	0.15 ns
Heat days	The number of days in a year with maximum temperatures above 30 °C	4	7	3	0.04 (0.01)	20.8 ***
Growing degree days	The heat sum above 5 °C	2215	2392	177	2.50 (0.40)	39.4 ***
Mean annual precipitation (mm)	The summed annual precipitation, averaged over a period (e.g. 1976-2005)	628	599	-29	-0.43 (0.43)	1.0 ns
Standardised precipitation-evapotranspiration index	A drought index that indicates predicted water deficit (negative values) and soil water surplus (positive values)	-0.1	-0.7	-0.6	-0.01 (0.002)	4.3 *

Supplementary material D4

Geographic variation in the functional traits measured in the current study of 45 provenances of *Eucalyptus ovata* across the eastern gene pool in Tasmania. See Table 6.2 for description of measured traits.

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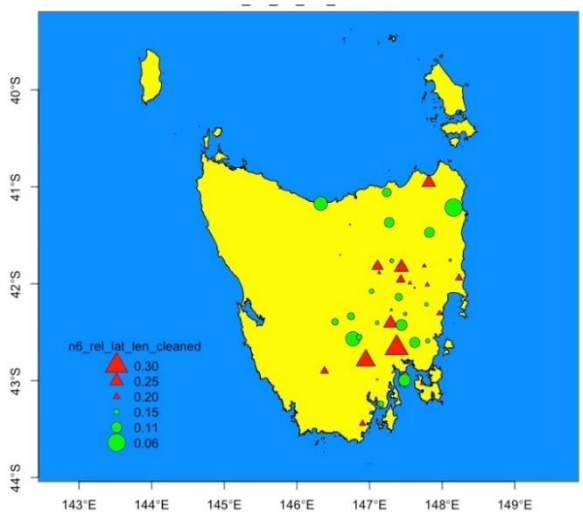
0.68
0.53
0.37
0.22
0.07
n6_SO_pa
0.82
0.65
0.49
0.33
0.16
0.00
n6_SR_pa
0.67
0.53
0.40
0.27
0.13
0.00
n10_stemDN
6.6
6.2
5.8
5.4
5.0
4.6
n10_internode_logit
-1.3
-1.4
-1.5
-1.6
-1.6
-1.7
n10_lignoCalc_sqrt
1.19
1.06
0.93
0.80
0.67
0.53
40°S
41°S
42°S
43°S
44°S
143°E
144°E
145°E
146°E
147°E
148°E
149°E


40°S
41°S
42°S
43°S
44°S
143°E
144°E
145°E
146°E
147°E
148°E
149°E
n6_rel_lat_len_cleaned
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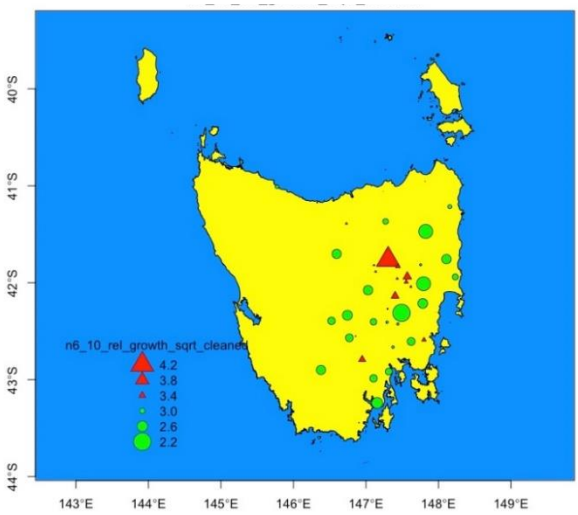
0.25
0.20
0.15
0.11
0.06


40°S
41°S
42°S
43°S
44°S
143°E
144°E
145°E
146°E
147°E
148°E
149°E
n6_10_rel_growth_sqrt_cleaned
4.2
3.8
3.4
3.0
2.6
2.2

Supplementary material D5

Association between the best additional home-site climate predictor variable (excluding TMXWW) with functional trait variation among provenances identified as under putative divergent selection (i.e. $Q_{ST} > F_{ST}$). Shown is the functional trait, the best climate predictor (see Appendix D1), the general slope of the curve (when significant), and the estimated degrees-of-freedom (eDF) of the thin-plate spline, the significance of the thin-plate spline after Bonferroni adjustment, and the percent (%) of variation explained (R^2) by the model including space (bivariate thin-plate spline function of latitude and longitude). Also shown is the difference between the R^2 of the model using TMXWW (Table 6.5) and the best climate predictor. Seedling traits are described in Table 6.2. Significance is shown after each test statistic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant ($P > 0.05$).

Trait code	Best additional climate variable						
	Variable	Slope	Curve	eDF	Test statistic	R^2 (%)	ΔR^2 (%)
Leaf crenulation	RDRYQ	-	linear	1.0	χ^2 =7.0 ns	32	10
Leaf thickness	TWMQ	negative	cubic	3.0	F = 14.1 ***	49	7
Leaf length	RRWETQ	-	quadratic	2.0	F = 2.1 ns	72	10
Leaf broadness	TMDR	-	linear	3.4	F = 1.5 ns	78	10
Number of expanded nodes	TMDR	-	cubic	2.9	F = 5.5 ns	51	4
Stem angularity	TWMQ	negative	linear	1.0	χ^2 = 13.8 **	47	2
Stem oils	TMNCW	-	linear	2.9	χ^2 = 13.1 ns	77	24
Relative lignotuber size	TDRYQ	-	linear	2.0	F = 1.2 ns	70	5

Supplementary material D6

Five discriminant axes capturing 93% of the functional trait variation among the 45 provenances of *Eucalyptus ovata* in Tasmania. Shown is the variance explained by each axis, the significance of the Pillai trace statistic tested using an *F* test, and the one-dimensional vector fitting of the functional traits under putative divergent selection ($Q_{ST} > F_{ST}$) into the discriminant space of each axis using the 'vectorfit' function of the *vegan* (Oksanen *et al*. 2017) package in R. The direction of each vector is shown relative to zero for the functional trait that had the highest variance explained (R^2). For example, stem oil gland develop increase as values on discriminant axis 1 become increasingly negative. Single vectors (i.e. for the second, third, and fourth discriminant axes) show a positive linear increase in these functional traits from negative to positive values along the discriminant axis. The R^2 and significance of the vector was calculated using 100,000 permutations of the data. Significance is shown after each test statistic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant ($P > 0.05$). See Table 6.2 for a description of each functional trait.

Discriminant axis	Variance explained	$F_{44,788}$	Trait vector fitting
1	41	10.8 ***	Stem oils (R^2 = 0.80 ***) < 0 > Relative lignotuber size (R^2 = 0.58 ***)
2	19	5.0 ***	Leaf broadness (R^2 = 0.77 ***)
3	15	3.9 ***	Number of expanded nodes (R^2 = 0.39 ***)
4	11	2.8 ***	Leaf thickness (R^2 = 0.58 ***)
5	7	1.8 ***	Leaf thickness (R^2 = 0.11 *) < 0 > Stem angularity (R^2 = 0.36 ***)

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017). vegan: Community Ecology Package. R package version 2.